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CONTENTS

THE FAUNA OF AN UPLAND POND AND ITS INFLOWING STREAM AT YSTUMTUEN, NORTH CARDIGANSHIRE, WALES

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(*With Plate 3 and 1 Figure in the Text*)

CONTENTS

1. INTRODUCTION

THE rivers and streams in the neighbourhood of Aberystwyth have been studied in some detail, notably by K. E. Carpenter and by J. R. E. Jones, but little attention has been given to the lakes and ponds which occur at the higher altitudes in the district. Small lakes are of fairly frequent occurrence at about the 1000 ft. level, having in the majority of cases had their origin from the mining industry, for which north Cardiganshire was noted during last century. A stream, if one were conveniently situated, was dammed to form a pool from which the water flow was controlled by sluice gates. Pond Lluest, at Ystumtuen in north Cardiganshire, is an example of such a body of water. The present paper gives a general account of the topography, of certain chemical properties of the water, of the main vegetation masses, and of the fauna in relation to the latter. A detailed account of observations concerning the dissolved oxygen is being published in the *Journal of Ecology* (1942).

2. TOPOGRAPHY

Pond Lluest is supplied with water from a reservoir, Lake Yr-Oerfa, which is at an altitude of 1085 ft. Yr-Oerfa is a lake of some 25 acres about 10 miles east from Aberystwyth, and is well stocked with good trout. A stream known as the Afon Tuen runs down from Yr-Oerfa for about 1000 yd. through uncultivated moorland, *Nardus* and *Molinia* pastures on peat (Newton, 1934, p. 50), to an altitude of about 950 ft., where it has been dammed,

so that it has broadened out to form a pool, Pond Lluest. The writer understands from local information that this was done about the middle of last century to improve the water supply of the Bwlchgwyn and Pen-rhiw mines. These have now fallen into disuse, and the pond, no longer required for the mines, was taken over by a group of anglers some 12 years ago and stocked with trout (*Salmo trutta* and *S. irideus*), which are at the present time very numerous. The ducks and geese of the neighbouring farm of Lluest-parc use the pond, and the moorhen (*Gallinula chloropus*) is occasionally seen, and nested in 1941. The sluice gates have been replaced by an iron grating which allows a steady outflow and tends to keep the water-level constant. This may rise considerably after heavy rainfall, but it only takes 2 or 3 days for the level to be restored.

The pond is a little over an acre in extent. There are no trees in its immediate neighbourhood. It is protected by the lie of the land from the most severe winds, but is nevertheless nearly always affected by wind to an appreciable extent, and is at times considerably disturbed by it. The rocks of the district are mainly Silurian grits and shales of the Valentian series (Jones, 1922), and are lacking in lime. The land is rather acid, and wherever water tends to accumulate *Sphagnum* bogs form.

3. Macroflora and bottom conditions

As indicated in Fig. 1, the vegetation of the pond is distributed in four more or less distinct areas of *Equisetum limosum*, *Potamogeton natans*, *Scirpus palustris* and *Sparganium minimum*. In July the *Equisetum* forms a very dense growth of vegetation over the north-west portion of the pond, growing out from the peaty margin. It merges at its easterly edge into a wide area of *Potamogeton* which extends out from the north-east bank into the deeper water. The growth of the *Potamogeton* is not as dense as that of the *Equisetum*. The southern half of the pond is mainly clear of vegetation at the surface, but patches of *Sparganium* extend along the south-east and a belt of *Scirpus* along the south-western side. The *Sparganium* forms a fairly dense growth of limited extent, its long strap-shaped leaves floating on the surface of the water; it does not reach to the shallow water of the actual margin. The *Scirpus* is not so much confined to one particular area as the other plants named above, but also grows in patches on the opposite side, among the *Potamogeton* plants in the shallow water near the margin. The patches tend to be small or to be intermixed with other vegetation. In various places close to the margin are patches of submerged *Littorella lacustris*.

The main current of the stream flows through the north-eastern portion of the pond; through the *Potamogeton*, but farther from the margin than the collecting station (B). The western portion of the pond is least affected. The only collecting station which is directly in the current is the stony bottomed region (F) near the outlet, with its grassy margin (G).

During the winter months the dying down of the vegetation affected the various areas in different ways. The *Equisetum* stems died and turned brown, but largely remained standing, and became covered with a dense growth of filamentous algae. The *Potamogeton* leaves decayed, nothing remaining visible at the surface of the pond, but the stalks remaining under the water. *Scirpus* and *Sparganium* areas were affected most, the plants dying down almost completely (the *Sparganium* first), supplying decomposing material to the pond bottom. By the end of April the spring growth was evident in all these areas.

New *Equisetum* stems were appearing above the normal water level replacing the old ones. New *Potamogeton* leaves were floating on the water. *Scirpus* and *Sparganium* shoots had appeared above the mud, but had not yet reached the surface of the water. *Potamogeton* and *Equisetum* began flowering towards the end of June, and *Sparganium* in the first week of July, all continuing to flower until the end of this month.
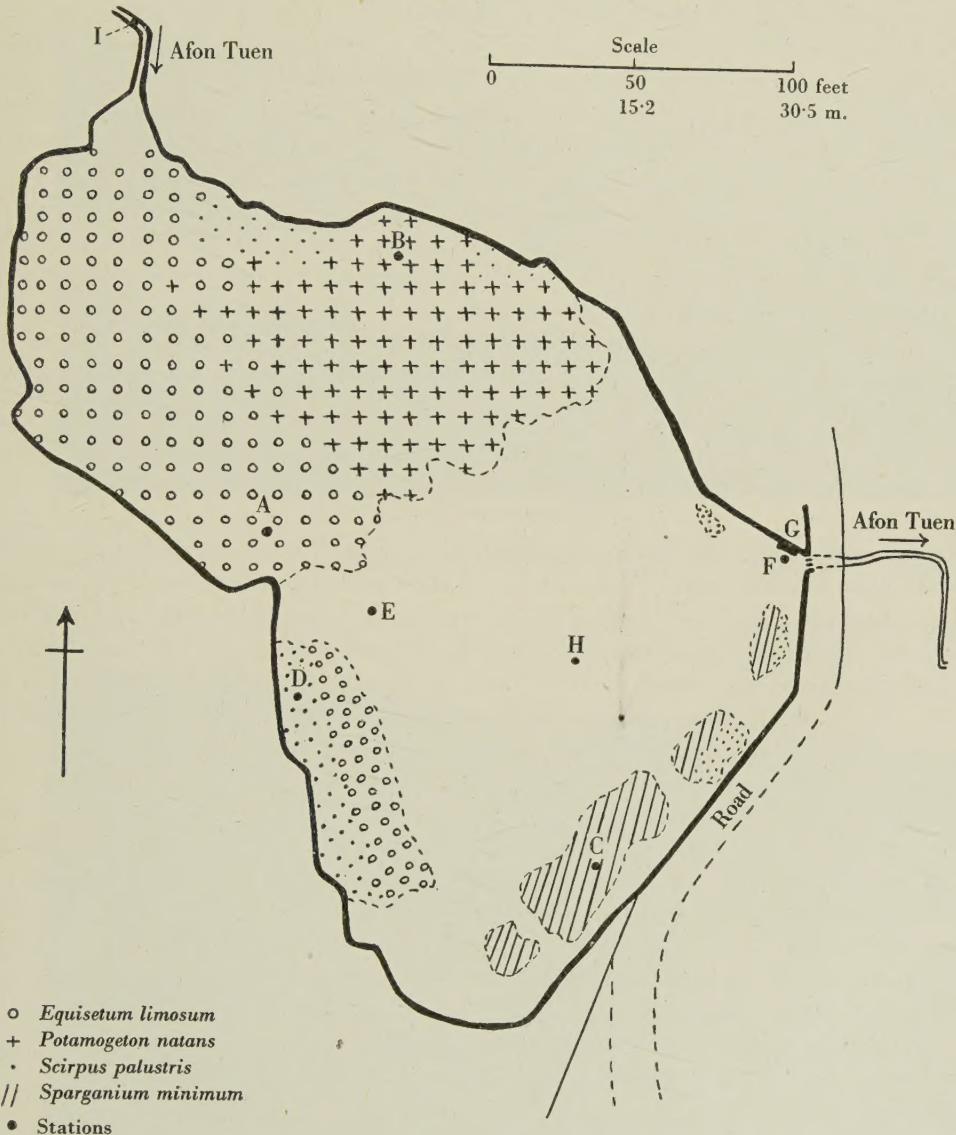
Fig. 1. Pond Lluest, Ystumtuen, with distribution of the main vegetation areas, and position of stations A–I.

The bottom of the pond is covered with fine mud and detritus, with generally an admixture of larger pieces of plant remains (largely *Equisetum*), to a depth varying from little more than a film to some 4 in., over a hard subsoil containing a good deal of gravelly

or stony material. Near the outlet, where there is a constant current of water, the mud does not settle easily, so that the bottom here is visibly stony. There is also a stony bottom along the south-east margin, which is the dammed side. Peaty land adjoins the pond on its north-western side.

By reference to Fritsch (1931, pp. 235–6) the area may be classified as a slightly acid moorland pond of oligotrophic type (Pl. 3, photos 1, 2).

The Afon Tuen flows swiftly over a stony bed. It varies from 1 to 2 ft. in width, and in depth from about 6 in., when 'normal', to 1 ft. when in flood. It never dries up, being constantly fed from the lake Yr-Oerfa. Its vegetation is very sparse; some of the stones carry algae, and macrovegetation is represented by occasional tufts of the moss *Fontinalis antipyretica* on the rock. The rate of flow of the water varies considerably from day to day and at different positions on the same day. During each of three periods of 'normal' water level, corks of various sizes, and other objects, thrown on the surface, travelled along a measured strip of 25 ft. at the rate of approximately 3 ft./sec. On another occasion the rate of travel was $2\frac{1}{2}$ ft./sec., and on yet another $3\frac{1}{2}$, with shorter lengths reaching 4 and perhaps 5 ft./sec. These figures refer to mid-stream. At the sides the rate of flow is less, and near the bottom it was on one occasion estimated to be about one-half that of the surface.

4. Notes on some properties of the water

(a) Hydrogen-ion concentration

A few pH estimations were made colorimetrically, using B.D.H. standard buffers. They were all made between 3 and 4 p.m. G.M.T. At the beginning of October 1940, and again in April 1941, the pH of the inflowing stream was 7·0 and that of the pond and outflowing stream 6·8. On 1 December 1941, the pH of the inflowing stream was 6·8, and that of the pond 6·8 (margin of *Equisetum* area), 6·2 (among decomposing *Potamogeton* leaves), and 6·6 (at outlet). On 9 April 1942, the stream and two stations in the pond, *Potamogeton* and 'open water', were 6·8. These values are usual in the vicinity.

(b) Calcium content

Estimations of the calcium content of the water (gravimetric estimation by precipitation with ammonium oxalate, etc.) indicated a calcium content of 6·20 mg./l. in mid-March 1941, and 6·46 mg./l. in mid-December 1941.

Weil & Pantin (1931, p. 77) describe the water from a stream at Wembury as 'a fairly typical hard water, rich in $CaCo_3$'. This water contained 64 mg. Ca/l. Plymouth tap water, on the other hand, containing only 1·7 mg. Ca/l., they describe as a very soft water. In the light of these figures the water of the Ystumtuen pond is clearly to be classed as a soft water. This is to be expected in view of the character of the rocks and soil.

(c) Dissolved oxygen and temperature

The results of weekly estimations of dissolved oxygen, estimated by the Winkler method, and taken over a period of fifteen consecutive months, showed that the water of the pond (average of five, sometimes six stations) and of the stream (one station) was on all occasions well oxygenated. The observations were made between 3 and 4 p.m. G.M.T. The maximum observed at this hour occurred on 21 December, when for the pond it was 14·1 mg. O_2/l., and for the stream 14 mg. O_2/l.; while the minimum, on 13 July, was 6·4

Photo 1. Pond Lluest, general view. The darker vegetation to the right of the pond is the *Equisetum limosum* area, into which the stream is seen entering; it leaves at the extreme left. (August 1942.)

Photo 2. Pond Lluest, showing the *Potamogeton natans* area with some *Scirpus palustris* growing amongst it, the open water area, and the outlet to the left of the middle line. (August 1942.)

for the pond and 7·8 for the stream. No great departure from 100% saturation was observed. For the pond it never exceeded 105%, and on only four occasions fell below 90%; and for the stream, once only above 109% and once below 90%. The temperature of the water samples for which the dissolved oxygen was estimated, as also of the air, was taken over a period of 13 months. The minimum water temperature noted (apart from January and February, when the pond was frozen over) occurred on 21 December, 1·2° C. for the pond and 1·8° C. for the stream; the maximum noted for the pond was 23·8° C., on 20 June, and for the stream 24·8° C., on 29 June. A full account of the observations concerning oxygen and temperature changes is given by the writer elsewhere (1942).

5. THE FAUNA

The fauna of the pond was studied from twenty-seven formal samples taken in July and October 1940, and April, July and August 1941, supplemented by a fair amount of general collecting at other times. The samples were obtained at the collecting stations A (*Equisetum* area), B (*Potamogeton* area), C (*Sparganium* area), D (*Scirpus* area), E (muddy bottom, free from macrovegetation), F (stony bottom near outlet, free from macrovegetation), and G (grassy margin near outlet), which are indicated in Fig. 1. The fauna of the inflowing stream was sampled in October 1940 by collecting for a distance of 100 yards above its entrance into the pond, and in July 1941 by examining the material collected from a square, 15 × 15 in., at a distance of 20 yards above its entrance.

The literature used in identifying the animals is listed at the end of this paper. The following authorities have kindly checked certain identifications: Mr A. E. Ellis the species of *Pisidium*; Dr E. Emrys Watkin the Crustacea; Mr W. Williamson the Hydracarina; Mr P. W. Carter, Mr E. H. Chater and Dr I. M. Wilson the plants. A sample collection of the animals is deposited in the Department of Zoology at Aberystwyth.

(a) *Methods of collecting*

The collecting apparatus employed in July and October 1940, and in April 1941, consisted of a hand net of cheese-cloth and a dredge. The former is about 15 in. deep with a semicircular opening about 11 in. in diameter, and screws into a stick 4 ft. in length. The dredge (Jones, 1941, p. 17) consists of a net, also made of cheese-cloth, about 16 in. deep with a circular opening 9 in. in diameter. This net is fitted into an iron frame to which a long piece of rope is attached. The weight of the frame causes it to sink as soon as it is thrown into the water. In all cases the catch was emptied into large jars of about 2 l. capacity, being in the case of muddy samples first washed in a sieve of 1 mm. mesh, and taken back to the laboratory for examination.

The *Potamogeton* and *Equisetum* stations were sampled by wading out into the vegetation and vigorously working the hand net through it at different depths. The dredge was then thrown out twice into the vegetation in deeper water than it was possible to reach with the hand net, and drawn into the bank. At the *Sparganium* station it was found that all the collecting could be done with the hand net, as this area does not extend beyond reach by wading. The frame of the hand net was sufficiently strong and sharp to press into the pond bottom. The *Scirpus* area is a fairly narrow belt and was sampled by twice drawing the dredge through its length.

The 'muddy bottom, free from macrovegetation' sample was taken by throwing the

dredge out into the pond as far as possible, from the west bank into a region practically free from macrovegetation. This bottom sample material, which contained a larger amount of mud than any of the others, required thorough washing through the sieve. The contents of two such throws constituted the sample. The 'stony bottom, free from macrovegetation' station was examined by turning over the stones and collecting from them by hand, by washing stones into the hand net and also by disturbing the bottom with the hand net. The Afon Tuen was examined by turning over stones in the water, the animals clinging to them being brushed off with the hand into the net, which was held immediately down stream. The stream bed immediately above the net mouth was well disturbed by hand, loosened animals being swept into the net by the current of the stream. A number of stones were also picked out and examined carefully for animals not dislodged by this means, and the net worked along the banks of the stream.

About 40 min. collecting was done on each occasion at each station by the above methods. The samples collected by one method on the same day from different stations are believed to be approximately comparable. This applies also to samples collected by the same method on different dates, but not to those taken by different methods, i.e. collecting for 40 min., with hand net and dredge, with quadrat of plants and bottom, and quadrat of plant fauna only.

For the seven samples obtained in July and August 1941 a more definitely quantitative method was adopted. The apparatus used was on simple lines, made by Dr J. R. E. Jones for this investigation. It consisted of a sheet of galvanized iron 18 in. wide, folded to form a four-sided frame surrounding a space 15×15 in. square, and 18 in. deep, the overlapping edges rivetted together. It was thus open above and below. This was placed over the patch to be sampled, preferably in water of insufficient depth to cover it completely. To ease this process among awkward vegetation, such as *Potamogeton*, individual plants were severed with scissors. The plants were then, in an area of vegetation, lifted out, and the bottom material was carefully removed by means of a strong cheese-cloth hand net attached to a rim having a straight sharp edge little shorter than the opening of the frame. The samples taken in this way confirmed qualitatively the previous ones, hardly anything new being taken. Some support was also forthcoming quantitatively; but the material collected from the vegetation in the frame was notably less, and that from the pond bed notably more. This will be seen by reference, for example, to the numbers of *Limnaea pereger* and of *Pisidium* in the samples from the *Potamogeton* area. The frame was found to work well in the shallow swift stream as well as in the pond; having been fixed in position in the running water, it was banked up with sods on the outside, and the contents removed at leisure.

In addition to the formal samples indicated above, collections were made from time to time at various places in the pond for other purposes. These were not sufficiently analysed for detailed record, but the writer's inspection of them confirms her impression that the formal samples represent fairly the macroscopic fauna of the pond.

(b) *The fauna of the stream*

The species obtained from the stream are listed in Table 1.

It will be noted that the fauna is markedly lotic, with an admixture of a few forms, e.g. *Lumbriculus variegatus*, brought in by sifting the sediment at the sides of the stream below the earth banks together with occasional grass roots.

Table 1. *Fauna of the stream*

	14 July 1941	16 Oct. 1940		14 July 1941	16 Oct. 1940
OLIGOCHAETA			ODONATA		
Lumbriculus variegatus Müll.	20	8	Enallagma cyathigerum Charp.*	—	1
Enchytraeidae	1	—	TRICHOPTERA		
Eiseniella sp.	5	—	Halesus radiatus Curt.†	3	—
HIRUDINEA			Sericostoma personatum Spence	3	—
Herpobdella atomaria Carena	—	1	Silo pallipes Fab.	3	—
MOLLUSCA			Odontocerum albicorne Scop.	8	—
Limnaea pereger Müll.	—	2	Hydropsyche pellucidula Curt.†	—	2
Ancylastrum fluviatile Müll.	1	5	Plectrocnemia sp.	6	—
Pisidium sp.	—	1	COLEOPTERA (Larvae)		
PLECOPTERA			Helmis sp.	1	—
Perlodes sp.	—	4	Helmidae sp. a.	8	—
Chloroperla sp.	—	1	DIPTERA		
Isopteryx sp.	3	1	Simulium sp. larvae	—	16
Leuctra sp.	4	7	Simulium sp. pupae	—	Numerous
Protonemura sp.	—	1	Forcipomyia sp.	1	—
EPHEMEROPTERA			Chironomidae colourless‡	2	1
Ecdyonurus sp. a.	3	7	Chironomidae§	10	—
Leptophlebia marginata L.*	—	12	Dicranota sp.	9	3
Baetis sp.	6	11			
Ephemerella sp.	22	—			

* Bred out by the writer.

† Bred out by Mr Henry Evans of the Department of Zoology, University College of Wales, Aberystwyth.

‡ Having dorsal papillae of ninth abdominal segment of the short '*Chironomus*' type.

§ Having dorsal papillae of ninth abdominal segment of the elongate '*Tanypus*' type.

(c) The fauna of the pond

The species obtained from the pond are listed in Table 2, which indicates their relative abundance at the various stations, and at different times of the year.

(d) Comparison of the fauna of the pond with that of the stream

In contrast to the stream fauna, that of the pond is in general of the type appropriate to still water with largely muddy bottom and considerable areas of vegetation.

One of the most numerous groups is the Mollusca, not in number of species but of individuals, the plant-loving *Limnaea pereger* and the mud-loving *Pisidium* taking the place of the stone-loving *Ancylastrum fluviatile*. Oligochaetes are numerous and there are a number of leeches. Hemiptera are well represented by various species of Corixidae, particularly *Sigara scotti*, and Odonata by the abundant damsel-fly *Enallagma cyathigerum*. On the other hand, Plecoptera, so well represented in the stream, are here represented only by a couple of specimens of the weed-loving *Nemoura*. Among the Ephemeroptera, *Chloëon*, a common pond genus, is the most abundant and has not been found in the stream; *Leptophlebia* is the next most common genus, one which occurs in both running and standing water. Mud-dwelling forms such as *Sialis* (Neuroptera) and red *Chironomus* (Diptera) are present in considerable numbers. Trichoptera are well represented by case-bearing vegetarian forms such as the swimming *Triaenodes bicolor* and *Leptocerus*, and the plant-loving *Phryganea* and *Limnophilus*; of the caseless forms, *Holocentropus*, characteristic of still water, is present in numbers.

(e) Biotic associations

Table 2 shows that the fauna tends to be zoned, species favouring some particular zone or zones rather than others. Their preferences can usually be correlated with food, suitable substrata for egg-laying, or some other environmental factor.

Table 2. *The*

(1) Sample was result of 40 min. collecting with net.
(2) Sample was entire content of frame 15 × 15 × 18 in. deep.
(3) Plants only, not bottom mud.
(4) Bottom adjoining *Sparganium*, free from macrovegetation.
(5) *Hibernicum* is the most numerous species of *Pisidium*. A sample of 201 specimens, collected from the four most populated stations, has been analysed by Mr A. E. Ellis and found to be composed of 89 % *hibernicum*, 10 % *subtruncatum* and 1 % *milium*.

	Potamogeton natans (station B)					Equisetum limosum (station A)			
	6 July 1940	9 July 1941	18 Aug. 1941	7 Oct. 1940	3 April 1941	9 July 1941	15 July 1940	5 Oct. 1940	3 April 1941
	(1)	(2)	(2), (3)	(1)	(1)	(2)	(1)	(1)	(1)
COELENTERATA									
Hydra vulgaris Pall.	2	1	2	1	—	—	—	—	—
H. viridissima Pall.	—	—	—	1	—	—	—	—	—
PLATYHELMIA									
Polycelis nigra Müll.	—	—	—	—	—	—	—	—	—
POLYZOA									
Cristatella mucedo Cuv., statoblasts	—	—	20	—	—	—	—	—	—
OLIGOCHAETA									
Stylaria sp.	5	—	10	37	27	—	4	52	500
Naidium sp.	—	34	—	—	—	17	—	—	—
Lumbriculus variegatus Müll.	—	—	—	—	—	1	—	—	—
Other spp.	1	—	—	1	—	—	—	—	—
HIRUDINEA									
Protoclepsis tasselata Müll.	—	—	3	—	—	—	2	—	—
Glossosiphonia complanata L.	2	—	—	—	—	—	—	—	—
G. heteroclita L.	—	—	—	—	—	—	—	—	—
Helobdella stagnalis L.	—	—	—	—	—	—	—	—	—
Herpobdella atomaria Carena	8	8	12	8	4	7	1	1	2
MOLLUSCA									
Limnaea pereger Müll.	157	41	56	312	165	—	60	27	9
Limnaea pereger Müll., egg masses	19	3	25	—	—	—	2	—	—
(5) Pisidium hibernicum Westerlund, P. subtruncatum Malm, P. milium Held	50	349	—	80	13	4	—	42	1
CRUSTACEA									
Ceriodaphnia megalops Sars, Eurycercus lamellatus Müll.; Cyclops fuscus Jurine; Ostracoda	Present, particularly in areas of vegetation								
Gammarus pulex L.	—	—	—	—	—	—	—	—	—
HYDRACARINA									
Hydrachna conjecta Koen. ♀	—	—	—	—	—	—	—	—	—
Limnesia undulata (Müll.) ♀	—	—	—	—	—	—	—	—	—
L. undulata (Müll.) ♂	—	—	—	—	—	—	—	—	—
Lebertia sp. ♀	1	—	—	—	—	—	—	—	—
Oxus strigatus (Müll.) ♀	—	—	—	—	—	—	—	1	—
Hygrobates longipalpis (Herm.) ♀	—	—	—	—	—	—	2	3	—
H. longipalpis (Herm.) ♂	—	—	—	3	—	—	2	12	—
H. longipalpis (Herm.) nymph	1	1	—	—	—	—	—	2	—
Neumania spinipes (Müll.) ♀	—	—	—	1	—	—	—	4	—
N. spinipes (Müll.) ♂	—	—	—	—	—	—	4	1	—
Piona coccinea (C. L. Koch) ♀	—	—	—	—	—	—	19	6	—
P. coccinea (C. L. Koch) ♂	—	—	—	1	—	—	—	7	—
P. rotunda (Kram.) ♀ ?	—	—	—	—	—	—	1	—	—
Hydrochoreutes ungulatus (C. L. Koch) ♀	—	—	—	—	—	—	20	—	—
H. ungulatus (C. L. Koch) ♂	—	—	—	—	—	—	5	—	—
H. krameri Piers. nymph	—	—	—	—	—	—	1	—	—
Acercus bullatus (Sig Thor) ♀	—	—	—	—	—	—	—	—	—
A. bullatus (Sig Thor) ♂	—	—	—	—	—	—	—	—	—
Forelia curvipalpus Viets	—	1	—	1	—	1	—	—	—
Arrenurus ornatus George ♂	2	—	—	3	1	—	2	6	—
A. neumani Piers. ♀	—	—	—	2	—	—	—	2	—
A. neumani Piers. ♂	—	—	2	2	—	—	—	42	—
A. bruzelii Koen. ♀	8	—	—	3	5	2	7	8	12
A. bruzelii Koen. ♂	—	—	—	—	—	—	—	—	—
A. crassicaudatus Kram. ♀	—	3	1	—	—	—	—	—	—
A. buccinator (Müll.) ♀	—	—	—	—	—	—	1	—	—
A. buccinator (Müll.) ♂	—	—	—	—	1	1	—	—	—
A. mülleri Koen. ♀	—	—	—	—	—	—	—	—	—
A. nymph	2	6	1	—	—	2	5	—	—
PLECOPTERA									
Nemoura sp.	—	—	—	1	—	—	—	—	—

fauna of the pond

(6) Bred out by Mr Henry Evans, of the Department of Zoology, University College of Wales, Aberystwyth.
(7) Having tergal processes of the '*fulvus*' type.
(8) Having dorsal papillae of ninth abdominal segment of the short '*Chironomus*' type.
(9) Having dorsal papillae of ninth abdominal segment of the elongate '*Tanypus*' type.

Muddy bottom free from macrovegetation (station E)					*Scirpus palustris* (station D)			*Sparganium minimum* (station C)					Stony bottom free from macrovegetation (station F)			Grassy margin (station G)		
9 July 1941	18 July 1940	12 Aug. 1941	7 Oct. 1940	15 April 1941	18 July 1940	5 Oct. 1940	9 April 1941	6 July 1940	18 Aug. 1941	10 Oct. 1940	9 April 1941	4 Aug. 1941	31 July 1940	16 Oct. 1940	15 April 1941	16 Oct. 1940	15 April 1941	Total
(2)	(1)	(2)	(1)	(1)	(1)	(1)	(1)	(1)	(2),(3)	(1)	(1)	(2),(4)	(1)	(1)	(1)	(1)	(1)	Total
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—	35	12	15	—	—	62
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20
—	—	—	—	—	—	—	—	—	33	20	—	2	—	—	9	25	2	726
10	—	21	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	85
2	30	—	—	4	—	—	1	10	—	—	6	73	—	—	4	12	2	145
—	—	—	—	4	—	—	1	—	—	—	1	—	—	—	—	—	—	8
—	—	—	—	—	1	—	—	—	—	—	—	—	2	1	—	—	—	9
—	—	—	5	—	—	—	—	1	—	—	1	—	—	1	—	—	—	10
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	3
1	3	—	6	1	—	—	1	8	1	3	5	22	37	8	4	—	—	100
—	—	—	2	1	1	5	6	11	4	1	6	6	10	5	3	—	1	113
2	15	1	81	10	14	22	39	7	—	4	—	1	12	40	10	—	72	1157
—	3	—	—	—	6	—	—	—	—	—	—	—	.9	—	—	—	—	67
977	200	767	370	480	200	425	601	151	—	97	231	768	10	40	2	—	10	5868

Present, particularly in areas of vegetation

—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	2 } 3
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1 }
—	1	—	—	—	3	—	—	—	—	—	—	1	—	—	—	—	—	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	2	—	1	5	—	1	2	—	—	1	2	—	—	—	2	1	22 }
—	2	—	2	4	2	—	—	3	—	—	—	—	—	—	—	3	—	33 } 69
—	—	—	—	1	5	—	—	1	3	—	—	—	—	—	—	—	—	14 }
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5 }
—	1	2	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	5 } 10
2	—	—	—	—	1	—	—	2	—	—	—	—	—	—	—	—	—	30 } 43
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13 }
—	1	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	23 } 28
—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	5 }
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	3
2	1	—	1	1	6	2	3	—	—	—	—	1	—	—	—	—	—	3 } 4
—	—	—	—	—	—	—	—	8	2	—	5	4	—	—	—	—	—	1 }
—	—	—	—	—	—	2	—	—	6	—	—	—	—	—	—	—	—	20
—	—	1	—	—	—	2	4	4	—	3	5	—	—	—	—	2	8	33
—	—	—	—	—	—	—	—	—	2	1	1	—	—	—	—	—	—	4 } 59
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	55 }
—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	75 } 76
—	1	—	—	1	2	—	—	7	—	—	—	5	—	—	—	—	—	1 }
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	7

Table 2

	Potamogeton natans (station B)					Equisetum limosum (station A)			
	6 July 1940	9 July 1941	18 Aug. 1941	7 Oct. 1940	3 April 1941	9 July 1941	15 July 1940	5 Oct. 1940	3 April 1941
	(1)	(2)	(2), (3)	(1)	(1)	(2)	(1)	(1)	(1)
EPHEMEROPTERA									
Chloëon sp.	10	3	—	2	2	—	40	—	2
Centroptilum sp.	—	—	—	—	—	—	—	—	—
Leptophlebia marginata L.	—	—	—	—	1	—	—	—	—
Caenis sp.	—	—	—	—	—	—	—	—	—
Ecdyonurus sp.	—	—	—	—	—	—	—	—	—
ODONATA									
Sympetrum danae Sulz.	1	—	—	1	—	—	—	—	—
Enallagma cyathigerum Charp.	95	22	4	43	27	1	1	—	1
Pyrrhosoma nymphula Sulz.	1	5	9	3	3	4	—	2	3
Aeschna juncea L.	—	—	1	—	—	—	—	1	—
HEMIPTERA									
Nepa cinerea L.	—	—	—	1	—	—	—	1	—
Velia currens Fab.	2	—	—	—	—	—	—	—	—
Gerris sp.	6	—	—	—	4	—	—	2	6
Sigara striata (L.)	—	—	—	—	4	—	—	2	6
S. distincta (Fieb.)	—	—	—	1	—	—	1	3	—
S. scotti (D. & S.)	—	—	—	—	6	—	5	41	22
S. venusta (D. & S.)	—	—	—	—	1	—	—	3	—
Sigara sp. young	7	35	2	—	—	12	100	—	—
Cymatia bonsdorffi (C. Sahlb.)	—	—	—	—	—	—	—	1	—
NEUROPTERA									
Sialis sp.	25	33	1	22	3	26	1	8	—
LEPIDOPTERA									
Nymphula sp.	2	—	—	3	—	—	—	—	—
TRICHOPTERA									
Phryganea sp.	34	3	1	7	1	2	8	31	8
Limnophilus rhombicus L.	—	—	—	—	5	—	—	—	15
Limnophilus sp.	—	—	—	—	2	—	—	—	3
(6) Halesus radiatus Curt.	—	—	—	—	—	—	—	—	—
Leptocerus sp.	—	—	—	2	2	—	—	—	—
Triaenodes bicolor Curt.	38	32	64	29	2	—	3	—	—
Oecetis sp.	1	—	—	—	—	—	—	—	—
Oecetis sp. (pupae)	1	—	—	—	—	—	—	—	—
(6) Hydropsyche instabilis Curt.	—	—	—	—	—	—	—	—	—
Polycentropus sp.	—	—	—	—	—	—	—	—	—
Holocentropus dubius Rambs.	—	—	—	5	3	—	—	3	—
Holocentropus sp.	65	—	10	5	4	—	16	5	6
Oxyethira sp.	—	1	—	2	—	2	5	3	—
COLEOPTERA (imagines)									
Haliplus fulvus Fab.	—	1	1	4	3	—	4	2	9
Haliplus sp.	—	—	—	—	—	—	—	—	—
Hydroporus palustris L.	—	—	—	—	—	—	—	—	1
Hydroporus sp.	—	—	—	—	—	1	—	—	—
Deronectes assimilis Paykull	—	—	—	—	—	—	—	—	—
Limnius tuberculatus Müll.	—	—	—	—	—	—	—	—	—
COLEOPTERA (larvae)									
Laccophilus sp.	—	—	—	—	—	—	1	1	—
Dytiscus sp.	—	—	—	—	—	—	—	—	1
(7) Haliplus sp.	2	—	—	—	—	—	—	—	—
Helmidae sp.	—	—	—	—	—	—	—	—	—
LEPIDOPTERA									
Nymphula sp.	—	—	5	—	—	—	—	—	—
DIPTERA									
Chaoborus sp.	—	—	—	—	—	—	2	—	—
Forcipomyia sp.	—	—	—	—	—	—	—	1	—
Corynoneura sp.	1	—	—	1	4	—	1	2	—
Chironomus sp. red	—	—	—	38	15	—	—	—	1
(8) Chironomidae, colourless	4	5	25	30	11	1	8	8	8
(9) Chironomidae	1	15	1	—	3	17	7	9	4
Chironomidae, pupae	—	1	—	—	—	6	9	—	—
Dixa sp.	—	—	—	9	—	—	8	5	—
Anopheles maculipennis Meigen	2	—	—	—	—	—	—	—	—
VERTEBRATA									
Triturus sp. (tadpole)	—	—	—	—	—	—	3	—	1
Rana temporaria L.	Present but not taken in the samples								
Salmo trutta L.	Very numerous but not taken in the samples								
S. irideus Gibbons	—	—	—	—	—	—	—	—	—
Anser anser (L.) var. domestica	Present								
Anas platyrhyncha L. var. domestica	Present								
Gallinula chloropus (L.)	Nested in 1941								

(*continued*)

Muddy bottom free from macrovegetation (station E)					Scirpus palustris (station D)			Sparganium minimum (station C)					Stony bottom free from macrovegetation (station F)			Grassy margin (station G)		
9 July 1941	18 July 1940	12 Aug. 1941	7 Oct. 1940	15 April 1941	18 July 1940	5 Oct. 1940	9 April 1941	6 July 1940	18 Aug. 1941	10 Oct. 1940	9 April 1941	4 Aug. 1941	31 July 1940	16 Oct. 1940	15 April 1941	16 Oct. 1940	15 April 1941	Total
(2)	(1)	(2)	(1)	(1)	(1)	(1)	(1)	(1)	(2), (3)	(1)	(1)	(2), (4)	(1)	(1)	(1)	(1)	(1)	
—	3	1	—	—	58	—	—	26	6	13	6	4	—	—	—	10	—	186
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	6	7
—	—	—	—	—	—	—	—	—	—	4	3	—	—	—	—	8	4	20
1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
3	—	—	9	—	3	2	2	18	3	17	11	4	9	—	2	16	1	294
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	13
1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	7
2	—	2	—	1	1	—	9	—	—	—	2	—	—	—	—	2	2	95
—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	3	10
2	4	14	—	—	105	—	—	75	1	—	—	1	—	—	—	—	—	358
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
67	—	115	39	49	32	31	42	11	—	—	13	16	—	—	—	2	—	536
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
2	2	—	—	—	4	1	—	2	—	—	2	1	—	—	—	—	—	109
—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	20	2	44
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	15	21
—	—	—	—	—	—	—	—	—	—	—	—	5	3	—	—	9	2	19
—	—	—	1	1	—	1	3	6	—	—	1	1	—	3	—	—	—	21
1	—	—	12	—	1	2	—	5	13	1	1	—	—	—	1	19	51	275
—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	4
—	—	—	—	—	—	—	—	3	—	—	—	—	4	—	—	—	—	8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
1	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2	—	—	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11
—	3	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	117
2	2	—	1	1	—	—	—	—	—	1	—	—	—	—	2	—	—	22
—	—	—	—	—	—	—	1	1	—	5	4	—	—	—	—	5	19	59
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
—	—	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
—	2	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	1	14
18	20	179	150	391	27	110	84	24	—	80	145	82	1	—	1	—	—	1366
—	—	7	6	9	—	15	4	—	12	7	11	—	—	1	12	—	1	195
9	2	18	—	19	8	—	—	4	9	—	10	—	—	—	4	—	—	140
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	22
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	3
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5

Present but not taken in the samples
Very numerous but not taken in the samples

Present
Present
Nested in 1941

The *Equisetum* and *Potamogeton* areas are those of richest plant growth. The *Equisetum* stems are crowded together and increase the stillness of the water. The flat-floating leaves of the *Potamogeton* and its tangle of submerged stems offer a very favourable habitat for some forms. In the *Equisetum* area the bottom mud is covered deeply with *Equisetum* debris. In the *Potamogeton* area the mud is more exposed and finds its way more easily into hand net and dredge. With the dying down of the vegetation of the pond the conditions in the *Equisetum* and *Potamogeton* areas are less materially affected than those in the *Scirpus* and *Sparganium* areas. The *Potamogeton* leaves decay but there remains a considerable growth of submerged living stem. The *Equisetum* stems remain standing after they are dead until the fresh ones grow up in the spring; the old stems become clothed with a mass of algal filaments. On the other hand the *Sparganium* and *Scirpus* disappear much more completely, so that the regions named after them become areas of open water.

Potamogeton natans area. The *Potamogeton* station is the richest in animal life. *Hydra vulgaris* and *viridissima* were found occasionally on the under surface of the floating leaves, and in the material collected at this station statoblasts of the Polyzoan *Cristatella mucedo* were taken. The area is the headquarters of *Limnaea pereger*, which, particularly in the case of younger individuals, finds the mass of submerged stems an appropriate perambulating ground, carrying a supply of algal slime ample for its needs. It is also the headquarters of the damsel-fly, *Enallagma cyathigerum*, the imagines finding suitable stems to pierce for the deposition of their eggs. Colourless *Chironomus* is found among the vegetation and *Holocentropus* is more numerous here than at any one of the other stations, living in silken nets under the floating leaves. Attached to these floating leaves the eggs of the Trichopteran *Triaenodes bicolor* and of the Hemipteran *Gerris* were found in considerable numbers in mid-August and were bred out in the laboratory towards the end of that month. The *Triaenodes* eggs occurred on the under surfaces arranged closely and neatly in hemispherical masses covered with jelly, the oblong *Gerris* eggs were in groups of one to two dozen, mostly on the upper, but sometimes on the under leaf surfaces. Also, and more frequently on the under than the upper surfaces, were capsules of *Herpobdella atomaria*, each containing 3 or 4 eggs or motile young; and occasional caterpillars of the Lepidopteran genus *Nymphula*, each in a shelter made by the attachment of a piece of leaf to the under surface. *Sialis* is here in the mud in abundance.

Equisetum limosum area. Hydracarina are well represented by both species and individuals. Corixidae are represented by five species, with *Sigara scotti* as the dominant one. Young *Sigara* individuals occur also in quantities in shallow open water at the extreme edge of the pond adjoining this region. Though not so rich generally in Trichoptera as the *Potamogeton* area, the *Equisetum* shares with it conditions suitable for *Phryganea*. The great number of *Stylaria* recorded in April is of interest. They were lying among the algal filaments with which the dead *Equisetum* stems were clothed; every dead stem, still standing upright, having its considerable contingent of *Stylaria*. This algal growth may also provide an explanation for the apparent preference of species of *Haliplus* for this area as compared with some of the others, since these are known to feed upon filamentous algae.

Muddy bottom free from macrovegetation. *Pisidium* is abundant here, also *Sialis*, and red *Chironomus*. *Lumbriculus variegatus* was well represented here in July 1940.

Scirpus palustris area. The dredge brought in a quantity of mud here, and after the dying down of the plant towards winter the area was not very different from the 'muddy

'bottom' area described above. It will be noted that its fauna is generally parallel to that of the latter. It is during summer and autumn, when the *Scirpus* is well grown, that some differences will be noted. Thus there were in July a number of *Chloëon*. There were also in July, in contrast to the 'muddy bottom' sample, a large number of young *Sigara*, perhaps largely because the sample was taken closer to the margin, in more shallow water, than the 'muddy bottom' sample.

Sparganium minimum area. As in the case of *Scirpus* the plant dies down in winter, and an approximation is thus made to the conditions of the 'muddy bottom', though the bed is here much harder than in either the latter or the *Scirpus* zone; there are stones, 1 to 3 in. across, below a thin layer of mud. This may account for the smaller number of *Sialis* and the comparative frequency of *Helobdella stagnalis*. Chironomids and small oligochaetes are present and are recorded as being fed upon by this leech. The bottom adjoining the *Sparganium*, which was sampled on 4 August, is of similar character, and of the same general character as that of the 'stony bottom free from macrovegetation'. Many more *Pisidium* were taken here by the quantitative apparatus than by the hand net.

Region near the outlet. The 'stony bottom free from macrovegetation' and the adjoining 'grassy margin' may be considered together. Here, where the water constantly flows towards the outlet, the stream forms, *Ecdyonurus*, *Polycentropus*, *Hydropsyche instabilis*, and *Halesus radiatus*, were taken. At the margin, *Stylaria* was present among the submerged grass, and *Lumbriculus variegatus* in the earth of the pond bank, water beetles were present, and Trichoptera were represented by *Limnophilus* and young *Triaenodes bicolor*. This patch is favoured by *Polycelis nigra*, the only Planarian taken in the pond, and this its only station. Leeches were plentiful, particularly the Gnathobdellid *Herpobdella atomaria*, and the Rhynchobdellid *Helobdella stagnalis*. The former is known to feed on small Oligochaetes and on Planaria, and the latter, together with *Glossosiphonia*, which is also present, on *Limnaea pereger*. The specimens of this mollusc taken from the pond bed at this station were at a much later stage in their growth cycle than those collected from vegetation.

(f) *Seasonal changes in the fauna*

Speaking generally, the same species are found in spring, summer and autumn, though at different stages in their growth cycles. The Hydracarina are exceptional in that a number of species are absent from the takings in April. The young stages of members of this group are parasitic, usually on insects. Their hosts in this pond were not ascertained.

Collections in October afforded a considerable contrast to those in July. As compared with July one's impression of the pond in October was that of a general nursery. The young of *Limnaea pereger* (of which there were a few in July, together with numerous egg masses) were present in great numbers; also those of *Pisidium*. Young individuals of *Enallagma cyathigerum* were not present at all in the July samples, but were numerous in October. Among the Ephemeroptera, *Leptophlebia marginata* and *Chloëon* were small. Among the Trichoptera, *Phryganea* and *Triaenodes bicolor*, which had been well grown in July, were now represented by young ones. Similarly the specimens of *Limnophilus rhombicus* were young. The growth change in the spiral case of *Phryganea* through the year is striking. In October, the young, though adopting the spiral arrangement were attaching the small pieces of plant stem by one end only, the other standing freely away and pointing obliquely backward to produce a broom-like effect; in April the material

and mode of building employed for older cases was being used, so that many represented an intermediate condition, in which the earlier portion was 'fringed' and the later portion of the more characteristic Phryganid appearance. In July the fully typical form had made its appearance. In *Sigara*, on the other hand, the young were dominant in July, only 9 out of 300 specimens being adult. All the specimens taken in October and April (55 and 57 respectively) were adult. 100 of the 115 specimens of *Sialis* taken on 12 August were young.

(g) *Notes on certain members of the fauna*

Polyzoa. Statoblasts of *Cristatella mucedo* were taken in the *Potamogeton* area in the middle of August, the small colonies with 3 or 4 lophophores emerging readily in the laboratory at the end of that month. This appears to be the first recorded freshwater Polyzoan for Cardiganshire.

Hirudinea. *Protoclepsis tasselata* is an interesting Rhynchobdellid species, considered rare in Britain. It is said to invade the nasal cavities of the throat region of ducks and other water fowl, As already mentioned the pond is used as a watering place for the ducks and geese of the neighbouring farm. Of the other leeches, *Helobdella stagnalis* and *Herpobdella atomaria* are fairly abundant, the former particularly favouring the stony-bottom localities; the latter is more generally distributed, and its egg capsules were taken on the leaves of *Potamogeton*.

Mollusca. *Limnaea pereger* was most numerous among the *Potamogeton* plants. Young individuals showed a strong tendency to favour vegetation, the older ones being frequently on the pond bed; this will be appreciated by reference to Table 3, and is no doubt corre-

Table 3. *Distribution of* Limnaea pereger *in relation to size, July* 1940

Size in mm.	Potamogeton	Equisetum	Muddy bottom free from macro-vegetation	Scirpus	Sparganium	Stony bottom free from macro-vegetation
1	2	16	5	—	—	—
2	31	27	5	1	—	—
3	26	11	2	1	—	—
4	63	2	—	1	—	—
5	17	2	—	—	—	—
6	10	—	—	—	—	—
7	1	1	—	—	—	—
8	—	—	—	—	—	—
9	—	—	1	—	2	1
10	—	1	1	1	—	1
11	2	—	1	1	2	1
12	2	—	—	6	2	2
13	—	—	—	3	1	1
14	—	—	—	—	—	1
15	—	—	—	—	—	3
16	2	—	—	—	—	2
17	1	—	—	—	—	—

lated with the higher proportion of egg masses taken at the *Potamogeton* station. *Pisidium* is very numerous in the muddy-bottom regions. Of the three species identified, *hibernicum* is the most common; as pointed out by Ellis (1940, p. 86) this is a species which tolerates soft water and is found at high as well as at low altitudes.

Crustacea. Planktonic Entomostraca are present but do not appear to be represented by any great numbers of individuals. The numerical emphasis is upon the Cladocera rather than the Copepoda, a feature shown by Nordqvist (1921, p. 76) to be characteristic of

oligotrophic ponds. The scarcity of *Gammarus pulex* may be noted, only two specimens being taken; it appears to be rare in the locality generally.

Hydracarina. The group is well represented and widely distributed in the pond, more being taken at the *Equisetum* station than elsewhere. *Forelia curvipalpis* is a new record for Britain.

Ephemeroptera. *Chloëon* spreads over the vegetation zones generally.

Hemiptera. *Sigara scotti* is the most common member of the order and is most numerous at the *Equisetum* station, and in the immediately adjoining region free from vegetation. It is described by Macan (1938; 1939, p. 24) as abundant in pools and peaty tarns in the Lake District. As indicated above, this part of Pond Lluest is bordered by peat.

Trichoptera. The order, of which there are a dozen species, is best represented in the *Potamogeton* area, where *Holocentropus* sp., *Phryganea* sp. and *Triaenodes bicolor* were common, the first two being found in lesser numbers in the *Equisetum*. *Limnophilus rhombicus* is another species of fair frequency at both these stations in April. The 'grassy margin' is also favoured by Trichoptera, particularly *Triaenodes bicolor* and species of *Limnophilus*. The tiny Hydroptilid *Oxyethira* is described by Mellanby (1938, p. 191) as 'not very common'. It has been found by the writer widely distributed about the Ystumtuen district. Its neat little flask-like silken case appears to be very resistent, no fewer than ninety-nine empty cases being counted in the 'muddy-bottom' sample for October. It is recorded by Jones from the river Ystwyth above Llanafan (1940, p. 375), and from the river Dovey (1941, p. 19).

6. SUMMARY

1. This paper gives a general account of the environmental conditions and the fauna of a pond and its inflowing stream at approximately 1000 ft. above sea-level in north Cardiganshire.

2. The water is slightly acid. Of the occasional determinations made for the pond the most usual pH value was 6·8, though in December, among decaying vegetation, 6·2 was recorded. Determinations for the stream gave pH 7 and 6·8.

3. The calcium content of two samples of pond water was 6·20 mg./l. and 6·46 mg./l., i.e. it is a soft water.

4. The water of both pond and stream is well oxygenated throughout the year. No great departure from 100 %, upward or downward, was recorded for observations taken between 3 and 4 p.m. G.M.T.

5. The fauna of the pond and stream are compared, the stone-clinging inhabitants of the latter contrasting with the vegetation-loving and mud-loving inhabitants of the quieter water of the pond.

6. The pond fauna was studied quantitatively from samples taken in April, July, August, and October, from seven collecting stations. The associations in different regions of the pond and their seasonal changes are described.

7. At least 98 species of animals were taken in the pond.

7. Acknowledgements

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STUDIES OF A SMALL MAMMAL POPULATION IN BAGLEY WOOD, BERKSHIRE

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(*With* 5 *Figures in the Text*)

1. INTRODUCTION

FOR an intensive study of a wild animal population some method of distinguishing the different individuals is essential. Birds have been studied for many years by a ringing technique. This was first applied to small mammals when Allen (1921) banded several bats in 1916. Marking methods for small rodents were developed independently by Johnson (1926) in the United States and by Zverev (1928) in the U.S.S.R. Many of the more important contributions to this technique have been included in a paper by Chitty (1937) and will not be mentioned here. The work described in the present paper is a continuation of Chitty's and is based on field observations in Bagley Wood, Berkshire, from October 1936 through February 1939.

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2. DESCRIPTION OF AREA AND FIELD METHODS

(*a*) *The trapping areas.* Bagley Wood lies just within the Berkshire boundary, about four miles west of Oxford. The section of the wood in which the work was carried on is shown in Fig. 1, based on the 1913 Ordnance Survey map (Berkshire sheet VI, 11; Oxfordshire sheet XXXIX, 11). Trapping was done in Milestone Piece (area A) and in Farringdon Gap (area B), where plantations of trees had been set out from 1919 to 1928. In these areas a relatively large number of distinct and easily separated types of habitat occurred within a few acres. These types are classified in Table 1.

(*b*) *The trapping grids.* Some uniform or standard method of trapping seemed advisable. The grid used by Chitty (1937) provided a satisfactory method for census. In a rectangular area of 150×200 yd., 36 posts had been set out in six rows of six posts each, thus forming nine smaller rectangles of 30×40 yd. each (Fig. 1). These smaller units were numbered from I to IX and each corner post was marked a, b, c, or d. This same grid was used in area A (without certain alternative posts used by Chitty) and covered 6·2 acres.

Table 1. *Habitat types in the trapping areas, Bagley Wood*

Habitat type no.	Characteristic primary growth		Characteristic second growth		Litter	Humus	Intensity of light	Area of occurrence
	Species	Density	Species	Density				
1	Sitka spruce (*Picea sitchensis*)	Heavy	Bramble (*Rubus fruticosus*)	Light	Medium	Medium	Dark	A and B
2	Larch (*Larix decidua, L. Kaempferi*)	Medium	Bluebell (*Hyacinthus non-scriptus*)	Light	Heavy	Heavy	Light	A
3	Western red cedar (*Thuja plicata*)	Heavy	Bramble	Light	Medium	Medium	Dark	B
4	Beech (*Fagus sylvatica*)	Medium	Bramble	Light	Light	Light	Light	A
5	Oak (*Quercus robur, Q. petraea*)	Medium	Bramble	Light	Light	Light	Light	A
6	Silver fir (*Abies alba*), Monterey cypress (*Cupressus macrocarpa*)	Heavy	Bracken (*Pteridium aquilinum*)	Medium	Medium	Medium	Medium	A
7	Larch, sycamore (*Acer pseudoplatanus*)	Medium	Bramble, bluebell, bracken	Medium	Heavy	Heavy	Medium	A
8	Larch, beech, chestnut (*Castanea sativa*)	Medium	Bluebell	Light	Medium	Medium	Medium	A
9	Larch, ash (*Fraxinus excelsior*), hawthorn (*Crataegus monogyna*)	Medium	Bramble, bracken, wood sanicle (*Sanicula europaea*), grass (*Deschampsia flexuosa*)	Heavy	Light	Medium	Medium	A
10	Ash, aspen (*Populus tremula*), birch (*Betula pendula*)	Medium	Bramble, bracken, wood sanicle	Heavy	Light	Medium	Medium	B
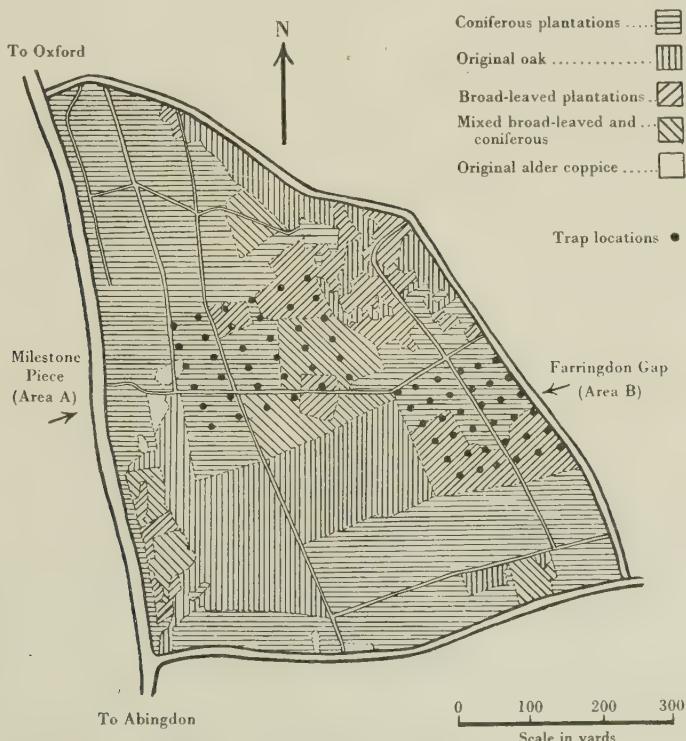
Fig. 1. Section of Bagley Wood in which trapping was carried on.

It was later felt that the varying distances between trap locations might give a false impression of the population distribution, and a second grid was constructed on area B to overcome this difficulty. This grid was laid out in the shape of a parallelogram, 150×150 yd., so that every trap location was 30 yd. from any adjacent location. This covered an area of 4·0 acres.

However, no significant differences were noted in the population distribution of the two areas which could be attributed to the different spacing of traps. Both types of grid appeared well adjusted to this method of trapping.

(c) *Extent of trapping.* The grids provided a series of fixed points, so that conditions were as nearly comparable as possible for each census sample in the study. The trapping procedure was identical on both grids. Three traps, of the Tring type used by Elton *et al.* (1931) and fully described by Chitty (1937), were set at each trap location, about 1 yd. from the post. Trapping was continued on each area for four successive nights per month, with one night at each of the four corner locations of the smaller units. All the nine *a* locations were trapped the first night, all *b*, *c* and *d* locations the following three nights. Thus 27 traps were in use every night of the experiment, and 108 trap-nights completed the monthly census of the area. Such censuses were made in each of twenty months in the period of the study. Exceptions to this procedure were made on two occasions, once when the number of traps was doubled, and once when the census covered eight nights instead of four.

(d) *Marking methods.* Each small mammal was marked by a metal ring on one of the hind legs. This method was developed and described by Chitty (1937). The rings were made of sheet nickel, numbered by means of a small metal stamp. Occasionally these rings proved too tight for the leg or adhered to the skin in such a way as to prevent proper circulation and to cause the foot to swell badly. In some of these cases it was possible to remove the ring, and animals which were so treated generally recovered. Frequently, however, it was necessary to amputate the leg. The majority of these individuals were subsequently recovered in later censuses and appeared to be in healthy condition.

(e) *Weight records.* After January 1937 animals were weighed each time they were caught. A fairly delicate spring balance, of the type used in weighing silks, was recalibrated and made accurate to 0·5 g. Enclosed in a wooden frame with glass front and suspended from a light tripod, it proved an extremely useful and not too bulky field instrument. A small wire basket held the animal while it was being weighed.

3. Population fluctuations and contributing factors

The main species caught were the wood-mouse (*Apodemus sylvaticus*) and the bank-vole (*Clethrionomys* (= *Evotomys*) *glareolus*). A few common shrews (*Sorex araneus*) and field voles (*Microtus agrestis*) and one water shrew (*Neomys fodiens*) were also caught.

Total figures for the material collected in this study are presented in Tables 2 and 3. In the twenty months in which trapping was carried on, 721 small mammals were caught and recaught 2460 times. The figures for area A and area B are nearly equal, although there is a slight divergence in species composition. These two areas approximated each other in size, and in habitat types, and each received the same amount of trapping. They were therefore as strictly comparable as field methods would allow.

Of the number of animals present in any particular month, those caught in the traps were perhaps a relatively small fraction. The comparative representation of the different species is not to be regarded as a true picture of the small mammal composition of the areas. The type of trap and bait used was not likely to capture such insectivores as *Sorex araneus* and *Neomys fodiens* with any degree of regularity. Only two species, *Apodemus sylvaticus* and *Clethrionomys glareolus* (referred to here as *Apodemus* and *Clethrionomys*), were taken in sufficient numbers for analysis. Table 4 presents data concerning these two species for each trapping period of the study.

Greatest numbers were generally caught in the early winter, but there was considerable variation from year to year. In the winter of 1936–7 the number of *Apodemus* trapped rose to a maximum of 87 in January–February, and although this fell to 68 in May the average for the year was well above any subsequent record. The 1937–8 peak was 51 in

Table 2. *Total number of individuals caught in Bagley Wood from October* 1936 *through February* 1939

	Total no. of individuals caught		No. caught on area A		No. caught on area B		Sex ratio		
	No.	%	No.	%	No.	%	♂	♀	?
Apodemus sylvaticus	377	52	214	59	163	45	197	180	—
Clethrionomys glareolus	310	43	143	39	167	47	157	145	8
Microtus agrestis	14		3		11		7	7	—
Sorex araneus	19	5	4	2	15	8	2	4	13
Neomys fodiens	1		—		1		—	1	—
Totals	721		364		357				

Table 3. *Total number of captures made in Bagley Wood from October* 1936 *through February* 1939

	Total no. of captures made		No. made in area A		No. made in area B		Sex ratio		
	No.	%	No.	%	No.	%	♂	♀	?
Apodemus sylvaticus	1606	65	925	75	681	56	814	792	—
Clethrionomys glareolus	817	33	303	24	514	42	455	351	11
Microtus agrestis	17		4		13		10	7	—
Sorex araneus	19	2	4	1	15	2	2	4	13
Neomys fodiens	1		—		1		—	1	—
Totals	2460		1236		1224				

November, after which numbers fell steadily until the beginning of the summer of 1938; in April 1938 there were only four individuals trapped on area B. By the autumn of 1938 the density began to increase again and reached another peak in November 1938, but this also fell off until February 1939, when the trapping stopped. The greatest numbers of *Clethrionomys* were caught in the early winter of 1937–8, with a maximum of 63 in November 1937. 17 of these died, and numbers declined to a low of 14 in May 1938.

The study did not continue long enough to determine whether these fluctuations were periodic in nature. More or less similar changes were recorded in Bagley Wood by Elton *et al.* (1931), who concluded that they might be part of a cycle in *Apodemus* but that there was no synchronization with the four-year cycle which had been suggested for *Microtus*.

It seems likely that with a limited number of traps some degree of competition for their use will exist between two or more species that are caught regularly. An increased capture of species A will automatically reduce the chances for capture of species B.

Consequently an increase in the numbers of species A caught would produce an apparent decrease in the numbers of species B, and vice versa. The degree of competition for traps and the consequent interdependence of the numbers of species A and B caught should be reflected in a comparison of the trapping results. From Table 4 it can be observed that parallel changes in the numbers of *Apodemus* and *Clethrionomys* occurred quite as frequently as the reverse. Statistical analysis of this problem could hardly be undertaken here without further knowledge of many unknown factors, but it would seem better to consider the material for the two species separately and independently.

A number of factors which probably contributed to these fluctuations are discussed below under separate headings.

(*a*) *Rate of survival on the areas.* The survival of *Apodemus* and *Clethrionomys* on the trapping areas is presented in Table 5. This is not equivalent to a life table, for the

Table 4. *Details of* Apodemus *and* Clethrionomys *caught on trapping areas A and B*

		Apodemus sylvaticus					*Clethrionomys glareolus*				
Year	Month	No. of indi-viduals	No. of females	Total no. of captures	No. of unmarked indi-viduals	No. of deaths in traps	No. of indi-viduals	No. of females	Total no. of captures	No. of unmarked indi-viduals	No. of deaths in traps
1936–7	Oct.–Nov.	47	24	62	47	0	17	10†	18	17	4
	Dec.	59	26	91	39	1	30	15†	35	25	1
	Jan.–Feb.	87	43	128	49	4	31	13†	34	15	2
	Mar.	78	34	139	19	1	25	11	29	8	3
	Apr.	—	—	—	—	—	—	—	—	—	—
	May	68	30	133	22	0	19	21	21	13	2
1937–8	Oct.	31	19	41	27	2	38	24	42	37	6
	Nov.	51	25	83	33	4	63	32	76	43	17
	Dec.	40	18	80	11	1	40	18	64	14	1
	Jan.	27	12	63	4	0	44	22	70	19	3
	Feb.	21	11	48	6	0	30	13	43	11	3
	Mar.	24	11	56	10	0	17	7	30	4	2
	Apr.	17	6	42	5	0	17	5	25	8	1
	May	17	9	35	8	0	14	5	22	4	1
	June	18	10	43	6	0	18	9	29	13	1
1938–9	Sept.	28	11	61	26	0	30	11	40	25	1
	Oct.	36	17	86	21	0	51	18	64	31	3
	Nov.	48	27	96	22	0	34	14	40	9	0
	Dec.	45	25	104	4	0	31	14	43	6	0
	Jan.	37	25	85	10	0	21	7	47	4	0
	Jan.*	23	15	42	5	0	16	7	23	3	0
	Feb.	36	22	88	3	0	15	6	22	1	0

* Re-trapping in area A only.   † Failure to sex all individuals.

following reasons: (1) the ages of the individuals when ringed could not be determined, and (2) disappearance from the areas may have been due either to death or to emigration.

Of the 353 *Apodemus* and 266 *Clethrionomys* which were ringed, 159 and 127 respectively disappeared before the next trapping period. The vast majority of these (cf. Table 5) disappeared after the initial capture. It has been suggested by Chitty (1937, p. 40) that the shock of initial capture may cause the death of a certain percentage of the trapped population. Of the 13 *Apodemus* and 51 *Clethrionomys* found dead in traps (Table 4), 10 and 41 respectively were new, unmarked individuals. There is not much evidence to indicate that an individual will, after release, die from the effect of trapping, but such a mortality factor cannot be overlooked. The other possibility, that of emigration, is discussed under a subsequent heading.

A fairly typical or regular decrease is observed in the numbers of *Apodemus* and *Clethrionomys* which 'survived' on the areas for one month or more after the first trapping

period. This is suggestive of a life table and may give some indication of the average length of life. Very little is known of actual length of life under field conditions. The longest period of survival recorded in this study was 15 months for *Apodemus* and 13 months for *Clethrionomys*. Burt (1940) records nearly 22 months survival in the field for *Peromyscus*, the American ecological counterpart of *Apodemus*. However, these are probably exceptions rather than the rule, and it is likely that the average survival is a much shorter period. Under laboratory conditions the observed length of life is naturally much longer. *Apodemus* is known to have lived more than two years in captivity (personal communication from R. M. Ranson of the Bureau of Animal Population) and Sumner (1922) recorded a life of five years and eight months for a captive *Peromyscus*. These observations agree with those of Burt (1940) that mice rarely reach 'old age' in the field.

Table 5. *Number of individuals 'surviving' on the trapping areas*

	Apodemus sylvaticus			Clethrionomys glareolus			
	Total	♂	♀	Total	♂	♀	?
Total no. of ringed individuals	353	184	169	266	138	121	7
No. which disappeared after initial capture	124	64	60	108	53	51	4
Others not surviving first trapping period	35	22	13	19	12	7	0
Survival in months after first period:							
1	194	98	96	139	73	63	3
2	149	71	78	97	52	44	1
3	110	53	57	65	35	30	0
4	67	29	38	32	19	13	—
5	48	21	27	19	13	6	—
6	23	7	16	7	3	4	—
7	16	5	11	5	3	2	—
8	10	4	6	3	2	1	—
9	8	3	5	3	2	1	—
10	5	3	2	3	2	1	—
11	3	2	1	3	2	1	—
12	3	2	1	2	2	0	—
13	3	2	1	2	2	—	—
14	1	0	1	0	0	—	—
15	1	—	1	—	—	—	—
16	0	—	0	—	—	—	—

(b) *Mortality*. No special observation was made of the predators in Bagley Wood, although weasels (*Mustela nivalis*), foxes (*Vulpes vulpes*) and owls were seen occasionally, each of which probably took its toll of the small mammal population.

Similarly, climatic conditions might be expected to affect the rate of mortality, but direct effects could not be calculated. From time to time animals were found dead in the traps, as is shown in Table 4. Only 13 deaths were recorded for *Apodemus*, and these occurred so sporadically that there was little suggestion of cause beyond the likelihood that certain individuals failed to adapt themselves to trap conditions and died from exposure. Occasional deaths among *Apodemus* in cold winter months were reported by Chitty (1937), who used similar trapping methods.

Clethrionomys died in the trap much more frequently than *Apodemus*. Chitty also recorded a higher death rate for *Clethrionomys* and suggested that it reacts much less favourably to confinement than does *Apodemus*. Table 4 shows a total of 17 deaths for *Clethrionomys* in November 1937, nearly three times as many as were recorded in any other month. In this and each succeeding month of the study, all dead *Clethrionomys*

were examined by Dr A. Q. Wells of the Department of Pathology. In a number of cases clear intranuclear inclusion bodies were discovered in the interstitial cells of the kidneys, but these were not definitely associated with the death of the animals. However, this may bear some resemblance to the type of mortality which Green and Larson (1938) have studied in the snowshoe hare (*Lepus americanus*). These animals were frequently found dead in the traps or died after a short period of captivity. Such individuals were found to be suffering from hypoglycaemia due to the failure of glycogen storage by the liver. This condition has been described as 'shock disease', as it is apparently 'stimulated to appear by the stress of trapping or captivity' (Green & Larson, 1938, p. 210). In February 1938 one specimen of *Clethrionomys* was recovered in a comatose state and was brought into the laboratory, where, at the suggestion of Dr R. G. Green who was present, it was injected with a solution of glucose; it revived and remained active for a short period. Post-mortem examination showed inclusion bodies in sections of the kidney. On a subsequent occasion, another *Clethrionomys* was similarly revived.

Table 6. *Records of movements made by* 14 *different* Apodemus sylvaticus
to places outside their original trapping area

Distance moved yd.	Time between captures days	Month
	Males	
420	4	Mar.
420	14	Feb.–Mar.
270	59	Mar.–May
260	25	Sept.–Oct.
250	5	Apr.
240	1	Sept.
230	23	Apr.–May
180–200	3	Feb.
180–200	58	Jan.–Feb.
150–180	6	Feb.
	Females	
190	4	Feb.
180–200	4	Feb.
120–150	1	Feb.
80	28	Jan.–Feb.

(c) *Population movements.* In the course of the work a number of fairly extensive movements made by *Apodemus* from one area to the other were observed; these are recorded in Table 6. Movements of over 400 yd. occasionally took place and on one occasion a distance of 240 yd. was covered in one day. The ability of this species to range widely must not be under-estimated, but such movements do not seem to be the general rule. In fact, there seems to be a tendency to restrict activity to a certain area (home range), though this does not imply that there is necessarily a display of territoriality on the part of *Apodemus*. Burt (1940) has produced good evidence of territorial behaviour in *Peromyscus*.

The tendency towards restriction of home range is shown in Tables 7 and 8, which record the maximum distance between trap locations at which any individuals were caught. The population is grouped according to the number of months between first and last capture. Individuals which were not known to be present on an area for at least one month have been excluded. Although movements of 250 yd. in area A and 280 yd. in area B could have

been recorded, the greatest observed in either area was 200 yd. Of the 194 *Apodemus* which survived on the areas for a month or longer, 144 or 75 % were apparently confined to home ranges of 100 yd. or less. An even greater restriction of range was observed in *Clethrionomys*, for of the 139 individuals which survived a month or more on the areas 116 or 83 % seemed to be confined to home ranges of 60 yd. or less. Chitty (1937) concluded that *Clethrionomys* did not range as widely as *Apodemus*, and he was able to record very few long movements. Such was also the experience in this work; one movement of 80 yd. and one of 300 yd. (No. E. 60) were the only records for *Clethrionomys*.

These recorded movements were probably affected by the trapping system, which artificially limited the distances at which the animals were caught. The problem of the animal-trap relationship is extremely complex and by no means fully understood.

Table 7. *The maximum distance between positions of capture of each* Apodemus sylvaticus *retaken within the same trapping area*

No. of months between first and last capture	Maximum distance between locations of capture, yd.									
	0	40	60	80	100	120	140	160	180	200
1– 2	4	25	25	12	6	2	2	—	3	1
3– 4	2	7	16	10	8	6	4	4	1	—
5– 6	1	—	5	11	6	3	1	1	1	—
7– 8	—	—	—	1	3	2	1	—	—	—
9–10	—	—	—	—	1	1	—	—	—	1
11–12	—	—	—	—	—	—	—	—	—	—
13–14	—	—	—	—	—	—	1	1	—	—
15–16	—	1	—	—	—	—	—	—	—	—
Total no. of individuals	7	33	46	34	24	14	9	6	5	2

Table 8. *The maximum distance between positions of capture of each* Clethrionomys glareolus *retaken within the same trapping area*

No. of months between first and last capture	Maximum distance between locations of capture, yd.									
	0	40	60	80	100	120	140	160	180	200
1– 2	17	32	20	6	—	2	—	—	—	—
3– 4	5	15	16	5	—	—	—	—	1	—
5– 6	—	4	4	2	1	1	1	—	—	—
7– 8	—	—	2	1	—	—	—	—	—	—
9–10	—	—	—	—	—	—	—	—	—	—
11–12	1	—	—	—	—	—	—	—	—	—
13–14	—	—	—	—	—	—	1	—	—	—
Total no. of individuals	23	51	42	14	1	3	2	—	1	—

(d) *Effect of immigration and emigration.* Some idea of the turn-over in the population can be gained from Table 4 which shows the number of new individuals in each monthly census. Large numbers of new individuals at the beginning of each trapping season are probably due as much to the additional young produced in the preceding summer as to the immigration of new individuals from the surrounding territory. In the non-breeding season, however, immigration probably assumes a major role. Of the 29 new *Apodemus* which appeared in March 1937 and 1938, 21 were adult males in breeding condition and were almost certainly immigrants.

Table 5 indicates that 45 % of the ringed *Apodemus* and 48 % of the ringed *Clethrionomys* were not caught after their first trapping period. A few of these were caught several times in the initial 4 days, but disappeared subsequently or were found dead in the traps. Of the 124 *Apodemus* which disappeared after the first capture, 64 were males

and 60 were females; 61 were adults, 35 immatures and 28 were not classified as to age. Of the 108 *Clethrionomys* which disappeared after the initial capture, 53 were males, 51 were females, and 4 were not determined; these included 52 adults, 45 immatures and 11 unclassified. This disappearance does not seem to be associated, therefore, with sex or age differences. It appeared to be rather evenly distributed throughout the period of study, and did not seem to bear any definite relation to the numbers of individuals found dead in traps. There is little indication of a mortality factor here, and emigration was probably responsible for some of the disappearance. In fact Table 5 suggests that the population may consist of two elements, one of which is relatively sedentary, and the other of which is essentially moving, possibly forced to do so by competition with other individuals for the necessities of existence.

Table 9.* *Percentage distribution of recorded weights of the* Apodemus
sylvaticus *population (both sexes, 1936–9)*

	5–9 g.	10–14 g.	15–19 g.	20–24 g.	25–29 g.	Total no. of measurements
Sept.	14·3	10·7	42·8	32·2	—	28
Oct.	3·0	41·8	37·3	13·4	4·4	67
Nov.	8·4	30·5	50·5	8·4	2·2	95
Dec.	—	36·5	55·3	8·2	—	85
Jan.	—	15·8	71·4	12·8	—	63
Feb.	—	9·4	64·2	24·2	2·2	95
Mar.	—	9·0	57·4	31·7	1·9	101
Apr.	—	—	30·0	70·0	—	17
May	—	—	30·6	61·2	8·2	85
June	—	16·7	11·1	61·1	11·1	18

Total   654

Table 10.* *Percentage distribution of recorded weights of the* Clethrionomys
glareolus *population (both sexes, 1936–9)*

	5–9 g.	10–14 g.	15–19 g.	20–24 g.	25–29 g.	Total no. of measurements
Sept.	6·7	26·7	46·6	20·0	—	30
Oct.	1·2	43·9	48·8	6·1	—	82
Nov.	—	50·5	41·1	8·4	—	95
Dec.	—	51·4	44·3	4·3	—	71
Jan.	—	55·4	44·6	—	—	65
Feb.	—	50·7	47·7	1·6	—	65
Mar.	—	30·9	66·7	2·4	—	42
Apr.	—	5·9	58·8	29·4	5·9	16
May	—	—	42·4	51·5	6·1	33
June	5·5	—	61·1	22·2	11·2	18

Total   517

* No weights were taken Oct. 1936–Jan. 1937 and a few animals escaped before being weighed in subsequent months.

(e) *Climatic factors.* Within the period of this study there were several abnormalities in the weather. The period of January, February and March 1937 was the wettest then on record, with a total deviation from the normal rainfall of 5·718 in. February, March and April 1938 were exceedingly dry, with March at its warmest and driest in 45 years. November 1938 was also the driest in a similar period. January 1939, with several snow-falls and a total precipitation of 4·442 in., was the wettest in more than 60 years. Table 4 indicates that the greatest numbers of *Apodemus* were caught in the abnormally wet period of 1937 and that the decline in numbers of trapped individuals coincided with the period of drought. It is a reasonable supposition that weather changes may influence the numbers of animals trapped, by limiting or encouraging their activity. The difficulty of

distinguishing between *actual* fluctuations in numbers and *apparent* fluctuations due to activity is one of the main problems of census technique.

(*f*) *Sex ratios and the breeding season.* The number of females in each monthly sample of the population is given in Table 4. The ratio of females to males varied considerably without much apparent regularity, although it approximated 1:1 for the total numbers of each species caught (cf. Table 2). A preponderance of males was noted in March, April and May and again in September and October. An unusual concentration of *Apodemus* females appeared in January and February 1939.

Sex ratio changes may be associated to some extent with the breeding season. A fairly rapid change in the size of the testes was observed in late January and by the end of February almost every male appeared to be in full breeding condition. Pregnant females were not recorded until April. Baker (1930) has shown fairly conclusively that the length of the breeding season is controlled by the condition of the female.

(*g*) *Age distribution.* The percentage distribution of the population in different weight groups is shown in Tables 9 and 10. All individuals under 10 g. were definitely young animals. Baker (1930) concluded that 14 g. for *Clethrionomys* and 15 g. for *Apodemus* were suitable weights at and above which all individuals could be classed as adults. In winter the populations of *Apodemus* and *Clethrionomys* were composed largely of individuals weighing from 10 to 19 g. each. After the onset of the breeding season there was a general increase in weight, with the majority of the population weighing from 15 to 24 g. each. By June a new generation was observed in the lowest group of from 5 to 9 g. while the heaviest group of from 25 to 29 g. was enlarged by the increasing number of pregnant females. The heaviest weight recorded was 29 g. for an adult male *Apodemus*.

4. Habitat occupation

It has already been suggested that there was a tendency for each individual to restrict its activity to a more or less definite area. It is not practicable to indicate the extent to which the habitat was occupied by diagrams of these individual ranges; a complete picture would be confusing, while at the same time the number of individuals per unit of space is too small to permit statistical treatment. However, it is reasonable to suppose that a capture at any trap position represents a certain amount of activity in that particular habitat, and that a cumulative record of all captures at all trap locations will give an aggregate picture of the relative density at the various points; this can then be translated into terms of habitat occupation. Such a picture is presented for *Apodemus* and *Clethrionomys* in Figs. 2 and 3.

If the distribution of individuals was assumed to be uniform throughout the areas, the number of captures at each trap location should be approximately equal and the range of values small. This was by no means the case. The distribution was tested by the formula

$$\chi^2 = \frac{S(x - \bar{x})^2}{\bar{x}},$$

where x stands for the observed values and $\bar{x}$ for the expected; this is the customary test for small samples of a Poisson series (Fisher, 1938, p. 60). The values of χ^2 obtained for the distributions in Fig. 2 were 158·8 for (*a*) and 174·85 for (*b*), and for those in Fig. 3 were 78·45 for (*a*) and 107·6 for (*b*). In each case the number of degrees of freedom (*n*) was 35.

Fisher (1938, p. 85 and Table III) states that where n is greater than 30, the significance of χ^2 must be tested by the expression

$$\sqrt{(2\chi^2)} - \sqrt{(2n-1)}.$$

The values obtained using the above expression were 9·51 for (a) and 10·39 for (b) in Fig. 2, and 4·22 for (a) and 6·36 for (b) in Fig. 3. If the conventional level of probability

(a) *Apodemus sylvaticus.*   (b) *Clethrionomys glareolus.*
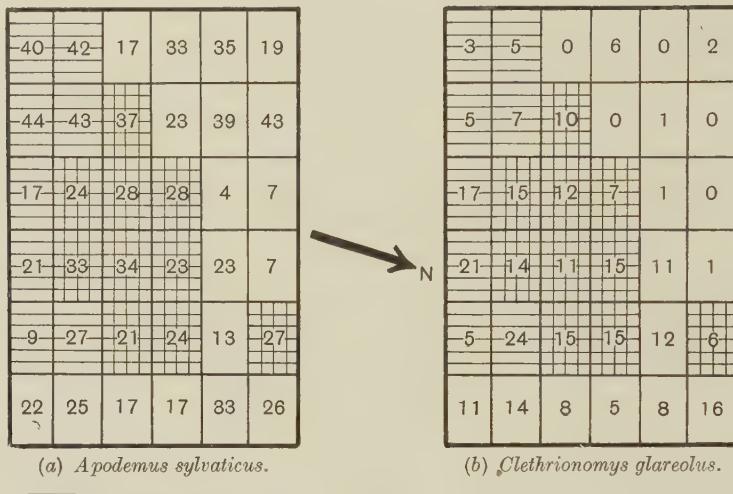
Thick bracken.   Scattered bracken.   No bracken.

Fig. 2. Distribution of captures in area A, 1936–9.

(a) *Apodemus sylvaticus.*   (b) *Clethrionomys glareolus.*
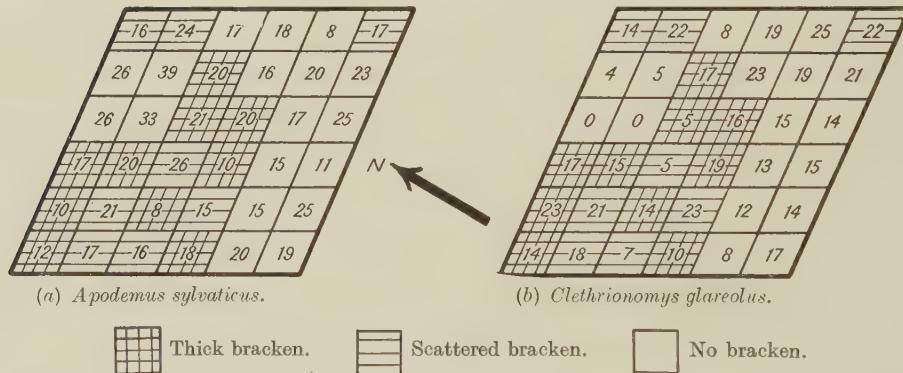
Thick bracken.   Scattered bracken.   No bracken.

Fig. 3. Distribution of captures in area B, 1936–9.

Note: In Figs. 2–5 the bracken is shown as 'thick' or 'scattered'. This distinction, though broadly true, is not based on a quantitative survey.

$(P=0\cdot05)$ be adopted, these values should not be greater than 2 if χ^2 is in accordance with expectation. The distribution of the *Apodemus* and *Clethrionomys* populations was therefore not a random one. Certain parts of the trapping areas were occupied to a greater extent than others.

Apodemus has already been shown to have a larger range than *Clethrionomys*. It was taken at every trap location in each area. Nevertheless the number of captures at several

locations was extraordinarily low. This was particularly true of locations in the beech and oak stands (habitat types 4 and 5), where there was little ground vegetation except for the bramble, and where the humus was light. No burrows were ever noticed in these stands and neither *Apodemus* nor *Clethrionomys* appeared to live there; yet it is strange that individuals passing through to other parts of the areas were not caught more often. In fact, it seemed likely that this territory was avoided and that the occasional captures represented stray individuals from near-by trap locations. Less apparently avoided, but also infrequently visited, were locations in young broad-leaved plantations (habitat types 8, 9 and 10). Highest catches of *Apodemus* were in the spruce, larch and cedar woods (habitat types 1, 2 and 3).

No *Clethrionomys* were taken in the spruce stand in area A (habitat type 1) and only a few individuals appeared in the cedar (habitat type 3). It also seemed to avoid the larch, beech and oak (habitat types 2, 4 and 5). The only factor that could be associated at all with its presence was the distribution of bracken (*Pteridium aquilinum*) (in habitat types 6, 7, 9 and 10). Table 11 shows the distribution of *Clethrionomys* captures for each

Table 11. *Distribution of* Clethrionomys glareolus *captures associated with the distribution of bracken* (Pteridium aquilinum) *based on trapping year*

	Area A		Area B	
	Bracken	Non-bracken	Bracken	Non-bracken
No. of trap locations	18	18	18	18
Total catches: 1936–7	32	7	71	27
1937–8	111	43	124	123
1938–9	64	46	87	82
No. of locations at which catches were made: 1936–7	13	6	18	10
1937–8	18	11	18	16
1938–9	16	12	17	16

trapping year at 'bracken' and 'non-bracken' trap locations. It is not suggested that bracken itself is the important factor, but it may be an indicator of conditions that are suitable to *Clethrionomys*. As is to be expected in studies of this sort, the material is of a suggestive rather than conclusive nature. In each trapping year, 'bracken' locations had uniformly higher catches of *Clethrionomys* than 'non-bracken' locations; and the proportion of 'bracken' locations at which catches were made was uniformly higher than that of 'non-bracken' locations. Yet this difference varied extremely from year to year, as did also the numbers of individuals captured. It was obvious that further analysis was necessary; this is presented in the following section.

The figures for *Apodemus* do not lend themselves to further analysis along these lines, since it was impossible to associate the distribution of this species with any known habitat factor. The possibility that the distribution of *Clethrionomys* was automatically limited by the distribution of *Apodemus* must not be overlooked. However, there was some evidence to indicate that *Clethrionomys* was active earlier in the evening or late afternoon than *Apodemus*; this would tend to give the former species the first opportunity at the traps and might offset any advantage secured by *Apodemus* in its ability to range more widely than *Clethrionomys*. Therefore, it appears justifiable to consider the distribution of *Clethrionomys* by itself.

5. The relationship of population fluctuations to habitat occupation

From the data presented in Table 4, differences in the population density of both *Apodemus* and *Clethrionomys* appeared to exist. In the case of *Clethrionomys*, four periods were selected to represent these different states, as follows: (1) from December 1936 through May 1937, a period of medium density, (2) from November 1937 through February 1938, a period of high density, (3) from March through June 1938, a period of low density, and (4) from September through December 1938, another period of medium density. Each period was comprised of the same number of trapping periods, and the different densities are relative to each other. The distribution of captures in these four population states is shown in Figs. 4 and 5.

It seemed likely that the differences in population density were variables which might affect the extent to which the habitat was occupied and might therefore be associated with the problem of distribution. Table 12 analyses the distribution of *Clethrionomys* captures as 'bracken' and 'non-bracken' trap locations in each of the four population states mentioned above. In period (1) there were considerably more captures in 'bracken' locations than in 'non-bracken' locations. In period (2) there were more captures at 'bracken' locations on area A, but fewer at similar locations on area B. In period (3)

Table 12. *Distribution of* Clethrionomys glareolus *captures associated with the distribution of bracken based on different states of population density.* (*Four trapping periods in each group*)

	Area A		Area B	
	Bracken	Non-bracken	Bracken	Non-bracken
No. of trap locations	18	18	18	18
No. of catches in different states of population density:				
(1) Medium: Dec. 1936–May 1937 incl.	26	6	64	23
(2) High: Nov. 1937–Feb. 1938 incl.	89	25	68	71
(3) Low: Mar.–June 1938 incl.	12	16	31	47
(4) Medium: Sept.–Dec. 1938 incl.	43	23	62	59
'Percentage of survival', i.e. (3)/(2)	13	64	46	66

'non-bracken' locations produced more captures than 'bracken' locations. In period (4) there was a return to greater occupancy of bracken habitats. This suggests that relative density and distribution are associated.

It will be observed that period (3) follows period (2) in immediate chronological order, and it will further be recalled from Table 4 that an unusually high number of *Clethrionomys* deaths was recorded during period (2). Evidence of any large-scale mortality is lacking, yet it is possible that some disease factor may have been responsible for the relatively rapid decline of the population from the apparent high density of period (2) to the low density of period (3). Such a factor would operate more thoroughly in a dense population than in a scattered one, and the proportion of those which survived would be correspondingly less. Table 12 suggests that such may have been the case; the 'percentage of survival' from period (2) to period (3) shows a correspondingly higher figure at locations where the density had been relatively low during the state of medium, and for area A at least, of high density.

This interpretation of the relationship of population fluctuations to habitat occupation differs from other theories. For example, Naumov (1936) has suggested that when a

population is at its lowest density it occupies only the most favourable habitats; that as the density increases, the pressure of numbers forces the population into less favourable habitats until a maximum density is reached when all possible habitats are occupied;
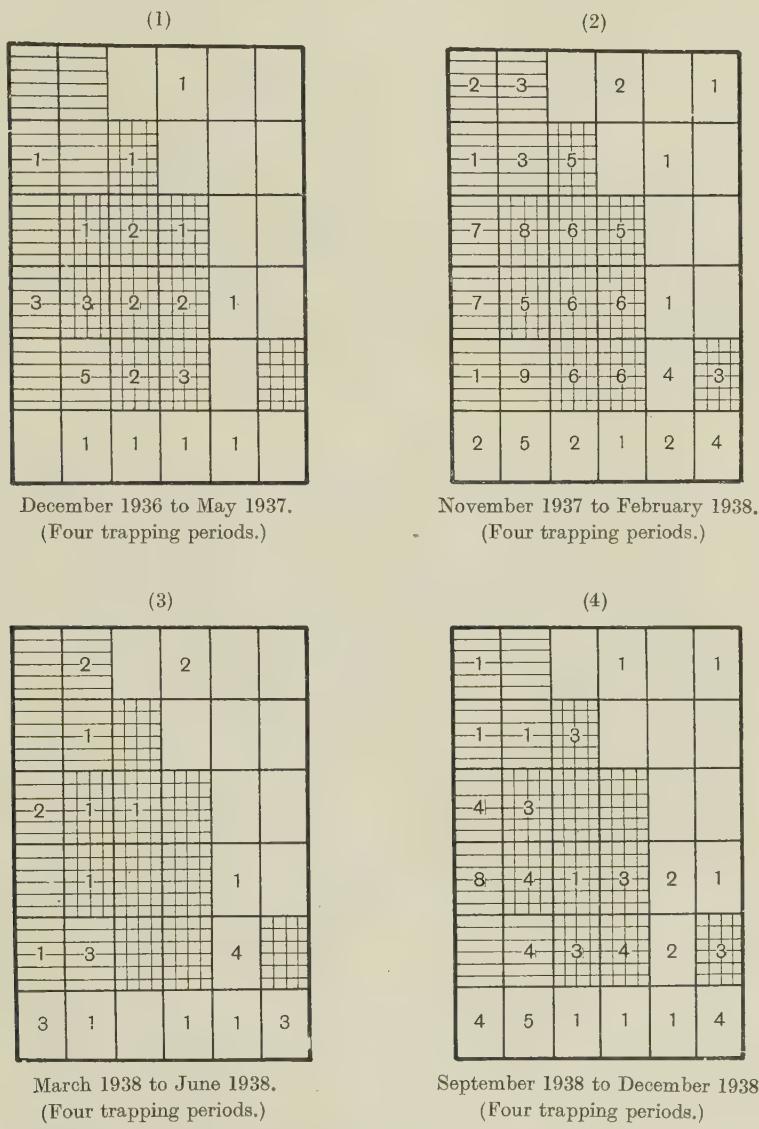
Fig. 4. Distribution of *Clethrionomys glareolus* captures in different states of population density. Area A.

and that periodic decreases of the population caused by migration or disease result in the occupation of only the most favourable habitats. The use of the term *favourable* seems somewhat misleading here. The new interpretation suggests that habitats which will

permit high densities of animal populations will also permit high densities of predators and parasites whose decimating effect may be so rapid as virtually to destroy those populations; habitats which will maintain only low densities may in the long run be essential to the survival of the species.
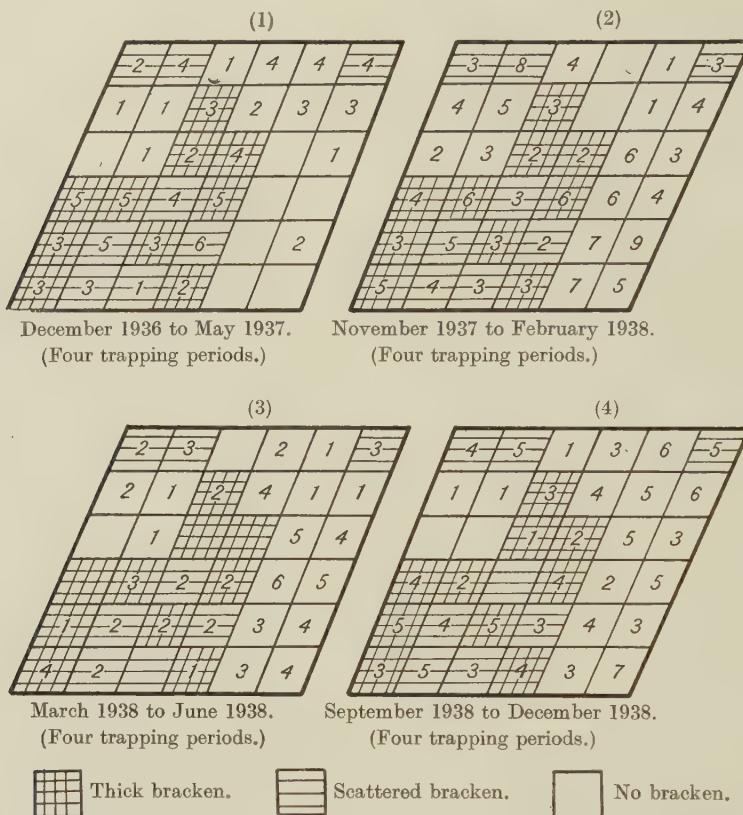
Fig. 5. Distribution of *Clethrionomys glareolus* captures in different states of population density. Area B.

6. Summary

1. A small mammal population in Bagley Wood, Berkshire, was studied from October 1936 through February 1939 by trapping and marking techniques.

2. The areas in which trapping was carried on provided a relatively large number of distinct and easily separated habitat types within a few acres. Two types of trapping grid were employed, and four nights of trapping completed the monthly census in each area. Individual mice were marked on the leg with a nickel ring and were also weighed.

3. The chief species studied were the wood-mouse (*Apodemus sylvaticus*) and bank-vole (*Clethrionomys glareolus*). Fluctuations in the numbers of both species were observed, and factors contributing to these changes are discussed. (*a*) About one-half of the population disappeared within one month after first capture. (*b*) The decrease in numbers caught to a very low relative density in the spring of 1938 (subsequent to a relatively high density and an increased number of deaths in traps) suggested some mortality factor. (*c*) *Apodemus*

was found to be a wider-ranging animal than *Clethrionomys*, but both species tended to restrict their activity to a fairly small home range. (*d*) Immigration and emigration apparently played a definite role in the population fluctuations. (*e*) It was suggested that weather changes may have affected the numbers of animals caught. (*f*) The sex ratio approximated to 1 : 1 for the total number of individuals caught, but males preponderated in the spring and autumn. (*g*) The populations of both species showed a general increase of weight with the onset of the breeding season.

4. Statistical analysis showed that the distribution of the population in the trapping areas was not random. Certain habitat types appeared to be avoided. The distribution of *Apodemus* could not be associated with any one habitat factor, but the greatest number of *Clethrionomys* were taken at trap locations in bracken (*Pteridium aquilinum*) areas.

5. The distribution of *Clethrionomys* appeared to be associated with its relative density. The population 'survival' from a period of high density to one of low density appeared to be greatest in those habitats which had normally maintained a low population density. It is suggested that habitats which will maintain only low densities may be essential to the ultimate survival of a species.

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THE WORM BURDEN OF SHEEP ON IMPROVED AND UNIMPROVED HILL PASTURES

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(With Plate 4 and 2 Figures in the Text)

1. INTRODUCTION

FACILITIES for investigating the effect of improved and unimproved hill pastures on the worm burden in grazing animals exist at Aberystwyth because of the experiments carried out by the Welsh Plant Breeding Station on the scientific management of grassland. The area where much improvement has been done is the Cahn Hill Estate situated about 16 miles from Aberystwyth and at an elevation of 900–1000 ft. This estate consisted originally of typical hill pasture, some of which has remained in its natural state while some has been improved by ploughing, by sowing with good quality herbage and by periodical treatment with nitrogenous manures. The effect of the different pastures on the weight and general condition of sheep grazed on the estate is being investigated by Mr Iorwerth Jones of the Plant Breeding Station, the sheep used by him being enclosed in two areas, one improved, and the other unimproved hill pastures. As in existing circumstances the setting up of separate experiments was not possible, it was decided to investigate the worm burden of these two flocks. Both flocks had been kept on their respective pastures for the whole of their lives except for a period during the winter when weather conditions made it necessary to transfer them temporarily to lowland areas.

It is a well-known fact that with the improvement of pastures heavier stocking becomes possible, and heavier stocking, one would expect, would increase the danger to infestation with parasitic worms. Taylor (1930) states that the infestation rate would increase as the square of the number of sheep per acre. This however is not necessarily the case in sheep on good pasture. Ross & Graham (1933) found that the improved condition of sheep on good pasture produced a greater resistance to worm infestation and incidentally a marked increase in mutton and wool production. Morgan (1933) studying the effect of heavy stocking on the worm burden in goats found that the improved quality of herbage under a system of rotational grazing increased their resistance to helminth infestation. Robertson & Fraser (1933) pointed out that overstocking accompanied by failure to move lambs on to fresh ground might give rise to heavy losses from helminths, and Fraser & Robertson (1933) later indicated that the carrying capacity of pastures is frequently limited by their infectivity and that the nutritional condition of the sheep is of extreme importance in resisting infestation. They found fewer worms in grazing lambs which received concentrated food as compared with those on pasture alone. Extra feeding with concentrates, however, may have the additional advantage of discouraging extensive grazing and thereby reducing the chances of infestation.

In the present study more conclusive results might have been obtained if the pastures could have been divided up so that each sheep was kept separately. This was apparently quite out of the question and so the flocks had to be treated as two units. However, the results obtained may prove of interest and are therefore put on record.

2. AREAS INVESTIGATED

Two areas were chosen for observation, an unimproved hill pasture (field A) and an improved hill pasture (field B). Field A (Pl. 4, Photo 1) includes an area of about five acres situated at an altitude of 1000 ft. The upper third of the field is very wet and boggy, the lower two-thirds slopes gradually downwards and is traversed by two very narrow streams with deeply cut overhanging muddy banks which form an excellent habitat for *Limnaea truncatula*. The vegetation is typical of an unimproved hill pasture. It consists mainly of *Molinia caerulea*, *Nardus stricta* and *Festuca ovina*, other grasses which are sparsely and unevenly distributed over the pasture being *Agrostis vulgaris*, *Poa trivialis*, *Holcus lanatus*, *Sieglingia decumbens* and *Anthoxanthum odoratum*. In the narrow sheep walks crossing the pasture *Poa annua* occurs, but there is not sufficient to form any appreciable grazing for the sheep. The upper wet region of the field is occupied mainly by *Molinia*, with large patches of *Sphagnum* in the wetter areas, this latter serving as a useful indicator of the degree of wetness of this part of the pasture. *Juncus squamosus*, *Calluna vulgaris*, gorse (*Ulex*) and bracken (*Pteridium aquilina*) are fairly abundant and there are such weeds as *Luzula campestris*, *Veronica montana*, *Galium saxatile*, *Ranunculus repens*, *Vaccinium myrtillus*, *Pedicularis palustris*, *Narthecium ossifragum* and *Potentilla tormentilla*. The food of the sheep consists of *Molinia* and *Festuca* together with small quantities of the other grasses and weeds mentioned. They will not eat *Nardus stricta*, though they tear up tufts of it.

Field B (Pl. 4, Photo 2) is an improved hill pasture of about three acres situated at an altitude of 900 ft. and about half a mile from field A. It slopes very slightly towards one end, is well drained with no pools, streams, or wet areas. It was originally part of a typical hill pasture. It was ploughed in 1936 and sown with Italian rye grass, perennial rye grass S. 23, timothy S. 48, and red and white clover. It was manured in 1935 and 1937. The pasture is of excellent quality and consists now of perennial rye grass S. 23, timothy S. 48, and white clover which have remained from the sowing in 1936, together with certain other grasses which have immigrated, in small quantities, from surrounding land, namely *Poa trivialis*, *Holcus lanatus*, *Agrostis vulgaris*, and *Festuca ovina*, also small quantities of *Ranunculus repens* and *Cerastium glomeratum*. The various species appear to be very evenly distributed over the pasture.

The stocking capacity of field B was considerably higher than that of field A: twelve sheep, or four per acre, were grazed on field B and eight sheep, or 1·6 per acre, on field A. The sheep were all of Welsh breed and of mixed regular ages from yearlings to 8 year olds. For the greater part of the year, from May until December, the sheep are on these pastures, but during the winter and early spring, when weather conditions are likely to be severe, the sheep from both fields are wintered together on the same lowland pasture, which is a poor one some miles away. The individual sheep were numbered and in May returned to their respective hill pastures. For nearly 5 months therefore all the sheep are subjected to the same conditions and for the remaining seven some live on improved and others on unimproved pasture. In the case of older sheep this process will have been repeated annually for several years, while the yearlings will have had only one winter on the lowland. The sheep which spend the summer and autumn on improved pasture are 50% better in every respect than those on the unimproved. The weights for the two pastures average respectively 90 lb. and 60 lb. In the former the wool is of better quality

and there is 100 % lambing as compared with 50 % lambing in the latter. The difference in condition is apparently due to the better quality and greater quantity of herbage on the improved pasture, which is sufficient to produce healthier sheep in spite of the heavier stocking.

In view of this difference in the general health and well being of the sheep, it was thought that an examination of their worm burden might give interesting results, especially as the sheep had all been together during the winter months.

3. Method of sampling and counting

Sampling. The pastures were visited at fortnightly intervals starting at the beginning of July and continuing until December. As it was not possible to obtain samples from each individual sheep, droppings were collected at random over the fields, twice as many samples being taken as there were sheep, that is twenty-four from the improved and sixteen from the unimproved. These were placed separately in glass stoppered bottles and brought back to the laboratory. Fresh droppings were always chosen so that they might be as representative of the flock as possible and the collecting was done in fine weather, the conditions during the time of sampling being of course the same for both fields.

Counting. The method used was a modification of the Stoll method and a combination of those used by Morgan (1933), and Peters & Leiper (1940). From each sample counts of eggs per gram of faeces were obtained by weighing 6·6 g., which was then thoroughly mixed with water with a mortar and pestle and the mixture run through a sieve of $\frac{1}{60}$ in. mesh to remove coarse particles. Anything left in the sieve was well washed and the whole solution passing through was poured into a measuring cylinder, the volume being made up to 200 ml. The solution was stirred in the measuring cylinder by twenty strokes with a plunger consisting of a rod with a perforated disk on the end. With a McDonald pipette 0·15 ml. of the fluid was then withdrawn, the strokes with the plunger being continued meanwhile. The 0·15 ml. was then transferred to a slide, covered with a large cover glass and all the eggs counted with the aid of a mechanical stage. Thus twenty-four series of two counts each were made for the improved pasture with twelve sheep, and sixteen series of two counts each for the unimproved with eight sheep. The average from these for each individual field respectively, when multiplied by 200, gave the number of eggs per gram of faeces. Details of the individual counts are not included in the table as space does not allow. The counts were all wet-basis counts though no extreme conditions were met with. The moisture content in faeces must naturally vary very greatly from time to time, but Peters & Leiper (1940) found that the variation in water content was not sufficiently large to alter the conclusions drawn from wet-basis counts; they were able also to confirm conclusions drawn from wet-basis counts by dry-basis ones.

During the counting the eggs were identified as far as possible. No single species of worm predominated at any particular time and the species were on the whole the same for both pastures. They included *Strongyloides papillosus* (Wedl), *Trichuris ovis* (Abildgaard), *Nematodirus* spp., *Haemonchus contortus* (Rudolphi), *Ostertagia circumcincta* (Stadelmann), *Chabertia ovina* (Gmelin), *Cooperia* spp., *Trichostrongylus* spp. and *Fasciola hepatica* Linn. (It is not possible in all cases to identify the species from the egg alone.)

Photo 1. Field A (in foreground, with sheep). Unimproved pasture.

Photo 2. Field B. Improved pasture.

4. RESULTS OF FAECAL EXAMINATIONS

The sheep had been on their hill pastures for nearly five weeks before observations could be begun; previously to this they had all been wintered together on the same poor wet low-land pasture. According to Taylor (1930) six weeks is the minimum time necessary for the completion of an average life cycle and so eggs appearing in the excreta when observations were first made at the beginning of July would be those produced by worms picked up before they returned to their summer pastures. The nematode and trematode infestations will be dealt with separately in the first instance.

Table 1. *Fortnightly counts of the number of eggs per gram of droppings from field A (unimproved pasture) and field B (improved pasture)*

	Field A (unimproved pasture)			Field B (improved pasture)		
Date 1941	Nematode eggs per g.	Fluke eggs per g.	Total no. of eggs per g.	Nematode eggs per g.	Fluke eggs per g.	Total no. of eggs per g.
2 July	1713	75	1788	317	4	321
16 July	1500	75	1575	263	4	267
30 July	513	138	651	142	13	155
13 Aug.	300	163	463	129	4	133
27 Aug.	75	150	225	121	13	134
10 Sept.	163	225	388	138	21	159
24 Sept.	113	200	313	121	33	154
8 Oct.	250	188	438	154	50	204
22 Oct.	200	275	475	146	29	175
5 Nov.	525	350	875	183	21	204
19 Nov.	525	338	863	183	7	190
3 Dec.	360	413	773	154	13	167

(a) Nematode infestations

Field A, unimproved pasture (Table 1, Fig. 1). The first count was made on 2 July when an average of 1713 nematode eggs per gram of faeces was obtained. This was the highest degree of infestation on this pasture during the whole period of observation. The second and third counts showed a fall in the number of eggs to 1500 and 513 per gram respectively. The fall continued steadily until it reached a minimum of 75 per gram in August, after which the number began to rise in stages to a maximum of 525 per gram in November. This seems to indicate that the highest degree of infestation occurred during the early months of the year while the sheep were on their poor winter pasture. When returned to their summer pasture which had been free from sheep during the winter the number of eggs gradually fell, since the sheep did not become reinfested at once. In quite a short time, however, eggs became distributed over the pasture and were picked up by the sheep, so that the initial fall in the number of eggs passed was followed by a rise which increased gradually as the source of infection increased and as the quality of the herbage decreased in the autumn. But at no time did it reach the height observed during the first examination in July.

Field B, improved pasture (Table 1, Fig. 1). The first count was made on the same day as for field A when an average of only 317 eggs per gram of faeces was found. As in the improved pasture, the number gradually decreased to a minimum in August after which there was a gradual rise to a maximum of 183 per gram in November, at the same time that the maximum appeared on the unimproved field.

The general outline of the curve is somewhat similar in both fields, an initial fall being followed by a rise reaching its maximum in November. The fall and subsequent rise on the improved pasture however is much less pronounced than on the unimproved. This seems to indicate that the sheep on the unimproved pasture are less resistant to infestation than the sheep on the improved. As already indicated, the condition of the sheep on the latter is 50% better in every way than on the former. The difference is most striking at the beginning of the experiment, shortly after both groups have been subjected to the same conditions during winter grazing. The greater rise in egg production in the autumn on the
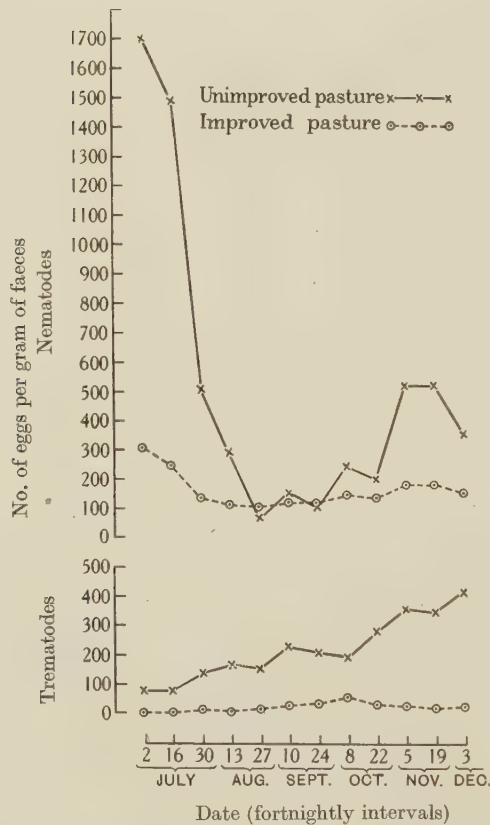
Fig. 1. Fortnightly counts of nematode and trematode eggs, per gram of faeces on unimproved and improved hill pastures.
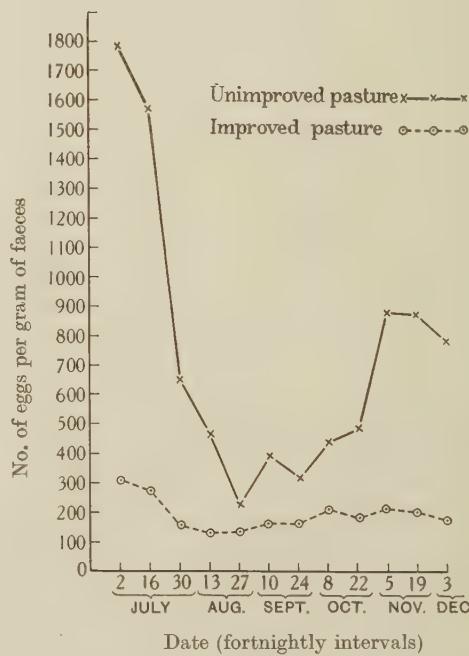
Fig. 2. Fortnightly counts of total egg content (nematodes and trematodes) per gram of faeces on unimproved and improved hill pastures.

unimproved pasture is due possibly to the lower resistance of these sheep and to a more extensive and closer grazing, as the herbage which is normally of poor quality becomes even poorer in the autumn. The sheep therefore have to eat more of it and may pick up very large numbers of eggs. The herbage on the improved pasture is very much more abundant and allowing for a slight decrease in quality during the autumn will be infinitely better than that of the unimproved field at any time. Possibly the sheep in this case do not need to eat so much or to graze so closely, therefore they may not pick up as many eggs or larvae. Lapage (1937) points out that malnutrition of the host will result in an

increase in egg production by worms parasitic within it and that the host's resistance which depends so markedly on its nutrition decreases the egg production by nematodes.

(b) *Trematode infestations* (Fasciola hepatica)

The unimproved pasture has been found to harbour *Limnaea truncatula* in fairly large numbers. They live on the muddy banks of the two narrow streams crossing the pasture and during wet weather they probably migrate out on to the surrounding pasture. On the improved pasture, which is well drained, no specimens of *L. truncatula* have been found. The presence or absence of the intermediate host of *Fasciola hepatica* is of course a vital factor in the spread of liver fluke infestations.

Field A, unimproved pasture (Table 1, Fig. 1). At the beginning of the experiment the number of fluke eggs was fairly low, being 75 per gram. There was a gradual though slightly irregular rise to a maximum in December. The early rise in the curve was probably due to the appearance of eggs from worms picked up on the winter pasture, as eggs begin to appear in the droppings about 12 weeks after infection. These eggs passed out by the sheep infect *Limnaea truncatula* on the pasture, cysts are later picked up by the sheep and the young worms grow to maturity in the bile ducts where they produce eggs which will appear in the droppings later in the autumn and which account for the rise in the egg count in November and December.

Field B, improved pasture (Table 1, Fig. 1). Very few fluke eggs were found in the droppings of sheep on the improved pasture at the beginning of the observational period, there being only 4 per gram. The number remained low with a slight and very gradual rise in September and October after which it fell again. The sheep as before became infested during the winter but as *L. truncatula* does not occur on the summer pasture, infestation cannot spread. There is therefore a fall in the number of eggs produced but a few eggs of course appear in the faeces as long as the sheep remains infested.

In the case of trematode parasites the main factor is the presence or absence of the intermediate host. This was absent on the improved pasture and so further infestation of the sheep was not possible. In spite of the fact that all the sheep were together during the period when the first infestation took place, there is an initial difference in the two fields which is probably due to the fact that sheep in poor condition become more heavily infested than those in better health. In the autumn of 1940 one sheep on the unimproved pasture died of fluke disease and in the autumn of 1941 one sheep showed fairly well-marked symptoms.

When added together the total worm count is even more markedly different for the two pastures (Table 1, Fig. 2). The initial fall and the subsequent rise in the number of eggs is very much smaller on the improved pasture. As already indicated, the difference seems to be accounted for by several factors, namely, the better health and greater power of resistance of sheep grazed on good pasture in spite of the considerably heavier stocking of 4 : 1·6, the better quality of the herbage, which is therefore not grazed so closely or so extensively; and the absence of *Limnaea truncatula* on the well-drained improved pasture.

SUMMARY

1. The worm burden of sheep on an improved pasture carrying four sheep per acre and an unimproved carrying 1·6 sheep per acre has been investigated, egg counts being made from samples of excreta collected on both pastures from July to December 1941.

2. The sheep from both pastures winter together on the same poor wet lowland pasture and return to their respective hill pastures each summer.

3. Infestation of the sheep takes place mainly in the winter. When they return to the hill pastures those sheep which spend the summer on the unimproved field show a high degree of infestation, viz. 1788 eggs per gram of faeces, while those on the improved field only 321 eggs per gram. In both cases there is an initial fall in the number of eggs followed by a rise as the sheep become infested again, but in all cases the degree of infestation is lower on the improved pasture in spite of the heavier stocking. The difference may be accounted for by the better health and greater power of resistance of sheep grazed on good pasture and to the better quality of the herbage, which is not therefore grazed so closely or so extensively.

4. Owing to the absence of *Limnaea truncatula* on the improved pasture there is here no increase in fluke infestation.

5. Acknowledgements

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ON THE BIRD FAUNA OF KAMBULE, MONGU, NORTHERN RHODESIA

By J. M. WINTERBOTTOM

(*With* 1 *Figure in the Text*)

CONTENTS

1. INTRODUCTION

The present study deals with the bird population of the Barotse National School station, near Mongu-Lealui, Barotseland, Northern Rhodesia, during the period from February 1939 to July 1941. Mongu itself stands on a hill of sand projecting into the Barotse Plain ('Mungu', the correct pronunciation of the name, is said to mean such a projection). Along the northern side of the hill runs a small stream ('Kanyonyo' in the local vernacular), which has eroded a little valley that goes back into the higher ground. Round the head of this valley, $2\frac{1}{2}$ miles from the hill on which the Government offices and residences are built, is the Barotse National School, the site of which is designated locally 'Kambule', meaning 'a source'. A sketch-map of the station is given to show the various points referred to in this paper.

In its original state, the whole of the higher ground was covered with what Trapnell & Clothier (**10**) call 'Baikiaea woodland'; but few trees of this species are left, for native gardens covered the site for many years before the school was put there in 1905. Although there are few *Baikiaea* trees, there are a number of others of different kinds, chiefly round the edges of the area. Of the indigenous trees, the most conspicuous are the muzaule (*Copaifera coleosperma*) and the mubula (*Parinari mobola*), the latter chiefly on the edges of the swamp that fringes the stream and the former mostly farther back. A considerable number of *Eucalyptus* trees have been planted along the border of the swamp. The stream itself, confined within two artificial channels but bordered, as indicated, by swampy areas, runs down the centre of the valley. At the western (lower) end of the valley, much of this swamp has been partially drained and is under cultivation, chiefly producing European vegetables. The rest of the area in covered with low, wiry grass (prominent species being *Cenchrus barbatus*, *Periotis indica* and *Aristida* sp.*) and bushes, the most conspicuous of these latter being isunde (*Baphia obovata*), mukuwa (*Copaifera baumiana*) and a species of *Bauhinia*. The total area is about 1100 acres. Although affected by its proximity to the Barotse Plain, the little valley is above even

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* I am indebted to Mr C. G. Trapnell, Ecologist, Department of Agriculture, for help in the identification of these grasses.

the highest flood level of the Zambezi and the flood waters cease about a mile from the western edge of the area here considered.

As comparisons will be made in this paper between the bird faunas of Kambule and those of the Jeanes School station, Mazabuka, and of Fort Jameson, previously studied by me (**13**, **14**, **16**), I include some geographical and meteorological data concerning the places (Table 1).
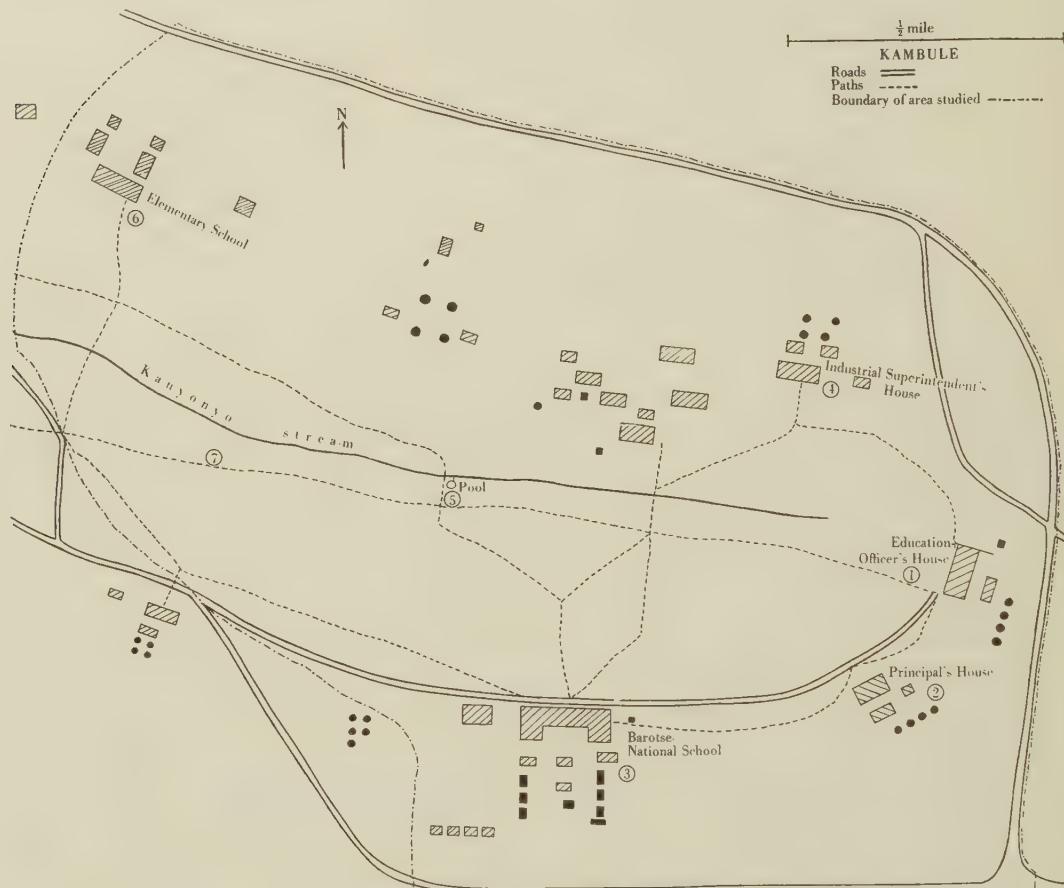
Fig. 1.

Table 1. *Geographical and meteorological data: Mongu, Mazabuka and Fort Jameson**

Place	Lat. S.	Long. E.	Altitude (ft.)	Mean rainfall (in.)	Absolute max. temp. °F.	Mean max. temp. °F.	Absolute min. temp. °F.	Mean min. temp. °F.	Original type of country
Mongu	15° 17′	23° 05′	3488	42·28	104	87·3	29	60·8	*Baikiaea* woodland
Mazabuka	15° 49′	27° 45′	3400	28·22	101	82·4	39	60·6	*Acacia* tree-grassland
Fort Jameson	13° 39′	32° 41′	3620	39·91	102	81·4	44	50·8	*Brachystegia* woodland

* Mongu and Mazabuka figures from Government Blue Books. Fort Jameson figures from Meteorological Reports, kindly supplied by the Senior Meteorological Officer, Air Training Group, Salisbury, S.R.

In addition to a direct count of the birds on part of the area (see below), the bird population was studied by means of daily lists of all species observed and by what I have called 'sample counts'. As these methods have been described in detail and their value assessed in a previous paper (**16**), I do not propose to go into them here. I there suggested that 300 counts per season is the minimum for reliable data for sample counts. The distribution of Daily Lists and Sample Counts by month and year are shown in Tables 2 and 4.

Table 2. *Daily lists: monthly distribution of counts*

Year	Totals	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1939	216	—	10	17	16	23	26	5	31	30	27	11	20
1940	184	5	14	15	25	31	13	18	4	—	21	18	20
1941	139	16	9	16	29	31	27	11	—	—	—	—	—
Totals	539	21	33	48	70	85	66	34	35	30	48	29	40

2. DIRECT COUNTS

No direct count of the whole area was attempted, nor, in the scrub region that forms a belt round the outside, could such a count give results of any value. A direct count was, however, made of the central section between the path that runs parallel with the south bank of the stream and the motor-road from the Education Officer's house to its intersection with the path already mentioned. The count was made on 9 June 1940, between 8.30 and 11 a.m. and the estimated area covered 240 acres. This consisted of grassland interspersed with trees, which increased in size and number from west to east and from north to south. North-west of the Barotse National School is the football field—a waste of sand stretching about half-way to the 'Pool'. West of this, a scrubby growth of *Bauhinia* and *Baphia*, 2–3 ft. high, occupied a good deal of the ground.

The total number of birds of all species counted in the area was 150, an average of 62 per 100 acres. This is much smaller than any previous figure for Northern Rhodesia (**11**, **12**, **15**), all of which agreed fairly well with the Moreaus' figure for Tanganyika (**8**); and is still smaller than Elliot's figure for an island in Lake Victoria (**1**). In addition to the general reasons considered below, the following special reasons for the low figure must be mentioned:

(*a*) The environment, while artificial in that many trees have been cut out and the grass and bushes kept short, contains no compensating advantages, such as fruit trees, artificial pools or crops of grain.

(*b*) The season of the year, June, is the time at which bird life is at its lowest ebb, for the winter visitors, of which the amethyst starling (*Cinnyricinclus leucogaster verreauxi*) is the most prominent, do not compare in point of numbers with the wet season visitors; and the grass is dry and brown, where it has not been burnt off.

The most numerous species were the cape turtle-dove (*Streptopelia capicola tropica*) and the pied crow (*Corvus albus*), each numbering 20 individuals.* It is, however, doubtful if more than three of the latter should properly be included, since the others were only flying over the area from the north compound and the garden to the south compound. They differ, however, from the case of the spur-wings in that they would

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* I have excluded from the count 25 spur-wing geese (*Plectropterus g. gambensis* (L.)), which flew over at 8.15, since these were merely on passage from the Zambesi plain to the Kande plain and could in no sense be regarded as part of the population of the area.

undoubtedly have descended had there been food visible on the ground, as there might well have been.

Next to the dove and the crow comes the amethyst starling, of which 13 were seen; followed by the white-bellied sunbird (*Cinnyris talatala*), estimated at 11—the sunbirds are so erratic in their movements that an exact count is impossible. Then came the drongo (*Dicrurus a. adsimilis*), 10 individuals; the southern helmet-shrike (*Prionops poliocephala*), one party of 8; the bronze manikin (*Spermestes cucullatus scutatus*) and the scarlet-chested sunbird (*Chalcomitra senegalensis gutturalis*), 7 each; and the black-headed bush-shrike (*Tchagra senegala rufofusca*), 6. The remaining species were:

5 individuals: yellow-vented bulbul (*Pycnonotus tricolor annectans*).*

4 individuals: rufous-bellied crombec (*Sylvietta rufescens pallida*), tawny wren-warbler (*Prinia mistacea graueri* Hart.), black-eared seed-eater (*Poliospiza mennelli*), the last being a 'first record' for the station and a 'farthest west' for the Territory.

3 individuals: grenadine waxbill (*Granatina granatina* (L.)†), glass-eye (*Camaroptera brevicaudata noomei*), black-headed oriole (*Oriolus monacha larvatus*), penduline tit (*Anthoscopus caroli robertsi* Haagner‡).

2 individuals: chin-spot flycatcher (*Batis m. molitor*), brown parrot (*Poicephalus meyeri neavei*), puff-back shrike (*Dryoscopus cubla hamatus*), ground-scraper thrush (*Geokichla litsipsirupa stierlingi*), racket-tailed roller (*Coracias s. spatulatus*).

1 individual: green-cap eremomela (*Eremomela scotops pulchra*), bateleur (*Terathopius ecaudatus* (Daud.)), lizard buzzard (*Kaupifalco monogrammicus* (Temm.)), yellow-fronted tinker-bird (*Pogoniulus chrysoconus extoni*), buff-breasted sunbird (*Cinnyris venustus falkensteini* Fisch. & Rchw.), grey-headed kingfisher (*Halcyon leucocephala swainsoni*), rock sparrow (*Petronia superciliaris*), red-eyed dove (*Streptopelia s. semitorquata*), purple roller (*Coracias naevius mossambicus* Dresser).

The total number of species observed was 31.

In considering these figures for direct counts, we must treat them with caution. First of all, we must not assume that because the bird population of these 240 acres is 150, that the 1100 acres of the whole station would only support 660. A census of the relatively small area between the path and the stream, for instance, would undoubtedly have yielded a much larger average. Numerous doves, bulbuls and manikins and several drongos were seen in the blue gums just across the path while I was counting the western end of the area.

Secondly, the direct count purports to give a cross-section of the bird population of an area at the time of the census. This may be of real significance during a Palaearctic summer, when the majority of the birds are breeding and a high percentage of the breeding birds are territorial. At other times, however, the bird population is essentially a fluctuating thing and no single cross-section can be of much value; though if conducted on the scale of those of Forbes & Gross (**3**, and the papers cited therein) this statement may need modification. In North America, however, the woodland density in the *Bird*

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* In dealing with the birds of an area in which almost no previous collecting has been done, some of the names used here may be liable to revision. As I have pointed out elsewhere (**17**), there is no adequate series of this common bulbul available for study, though Mr C. M. N. White and I are endeavouring to remedy the omission. Dr Austin Roberts, who described *annectans* from the Sesheke-Livingstone border, considers Mongu birds are very similar.

† Perhaps an undescribed race.   ‡ Or a new race.

Lore censuses (**9**) varied from 48 in grazed sugar maple to 950 in second-growth hard-wood and field; while a maple-birch bog forest which only supported 15 pairs in 1937, supported 40 in 1939. These remarks suggest that only a count repeated at frequent intervals can give an adequate idea of the bird population of a given area, since the numbers of the bird fauna are varying so much. Over a small area (21 acres), this is borne out by a previous study of mine (**12**), where the numbers of one species varied during 5 days from 0 to 30; of another from 3 to 14; and of a third from 8 to 19; while the total number of birds varied from 47 to 80.

For these reasons, therefore, I am not inclined to attach much importance to direct counts, especially of small areas; and unless they are repeated at least weekly, I consider that they give a picture more misleading than that offered by the methods described below. Such a repetition was physically impossible and the conditions during the height of the rains would, in any case, have militated so severely against accuracy that the value of the count would have been extremely dubious.

3. Daily lists

Daily lists were kept for 539 days, and 152 species were recorded. This compares with 163 species in 596 days in Fort Jameson during 1935–8; and 175 between 1932 and 1938, on 1231 days. At Mazabuka, 119 species were noted on 208 days, but the period covered was less than a year.

The results of dividing the 152 species into groups on the basis of occurrence, such that group A comprises species occurring in 1–20% of the counts, B in 21–40%, C in 41–60%, D in 61–80% and E in over 80% are shown on a percentage basis and with figures from elsewhere, in Table 8. The actual figures are: A, 107; B, 16; C, 10; D, 7; E, 12. They agree with the expected formula of $A > B > C \gtreqless D < E$. Comparing the results with those for Fort Jameson, we find that there is one less species in group E and 24 less in group A. In Table 3 I give the seasonal percentage occurrence of the 29 species in groups C, D and E. I have kept the same seasons as in Fort Jameson—May–October, dry and November–April, wet, both inclusive; though actually rain rarely falls in Barotseland in April. It will be noted that while the average number of species per day in the dry season is slightly less than at Fort Jameson, the number in the rains tends to be more—only the last rainy season producing an average below the Fort Jameson figures. Nevertheless, the average aggregate is only 29·7 per day, as against 32·5 for Fort Jameson.

4. Sample counts

For these, seven stations were used, their positions being shown on the accompanying map. The distribution of counts per month is shown in Table 4. In all, 2006 counts were made, as against 1551 and 1970 in two approximately equal periods of time in Fort Jameson. In addition to one blank month (September 1940), there were nine other months in which the number of counts fell below 50 and I have therefore used the figures seasonally only. Table 5 gives the results for the more prominent species. In Table 6, the monthly percentages for April 1940 and 1941, and for May 1939, 1940 and 1941, are given.

The sample count figures bring out some well-marked seasonal fluctuations, though only the four middle seasons give really reliable figures, the figures for 1938-9 wet and 1941 dry seasons being rather few and relating only to the end and the beginning of the

Table 3. *Daily lists: seasonal percentages of prominent species*

Species	Wet 193–89	Dry 1939	Wet 1939–40	Dry 1940	Wet 1940–1	Dry 1941
Batis m. molitor (Hahn & Kust.)	74	89	81	87	87	91
Camaroptera brevicaudata noomei Gunn. & Robts.	4*	81	86	91	93	80
Centropus cupreicaudus Rchw.	56	16	78	44	71	35
Chalcomitra senegalensis gutturalis (L.)	100	69	32	48	63	59
Cinnyris talatala (A. Smith)	11*	96	94	99	81	96
Corvus albus Müll.	93	93	89	98	97	97
Dicrurus a. adsimilis (Bechst.)	93	99	94	98	97	100
Dryoscopus cubla hamatus Hartl.	96	89	92	88	82	81
Eremomela scotops pulchra (Boc.)	15	61	60	55	48	60
Erythropyga zambesiana near munda† (Cab.)	70	79	80	84	88	87
Geokichla litsipsirupa stierlingi Rchw.	15	33	31	29	56	83
Glaucidium perlatum (Vieill.)	52	56	69	66	16	13
Halcyon c. chelicuti (Stanley)	7	23	38	32	83	81
H. leucocephala swainsoni (A. Smith)	74	56	69	66	16	0
Hirundo r. rustica L.	26	0	30	9	44	0
Lophoceros nasutus epirhinus (Sund.)	89	84	74	82	87	86
Merops superciliosus persicus Pall.	51	1	34	1	43	0
Malaconotus poliocephalus hypopyrrhus Hartl.	81	64	63	38	57	29
Oriolus monacha larvatus Licht.	100	98	94	96	87	97
Otus s. senegalensis (Swains.)	89	85	63	80	78	52
Petronia superciliaris (Blyth)	44	57	60	54	56	10
Phoeniculus purpureus marwitzii (Rchw.)	7	11	8	61	74	74
Pogoniulus chrysoconus extoni (Layard)	96	96	80	88	97	99
Poicephalus meyeri neavei C. Grant	74	89	80	92	90	97
Prionops poliocephala (Stanley)	22	60	62	61	81	80
Pycnonotus tricolor annectans (Robts.)	100	98	95	100	100	100
Spermestes cucullatus scutatus Heugl.	22	40	63	63	69	16
Streptopelia capicola tropica (Rchw.)	100	98	92	96	96	99
S. s. semitorquata (Rüpp.)	89	67	55	82	63	86
Sylvietta rufescens pallida (Alex.)	37	35	38	69	63	55
Tchagra senegala rufofusca (Neum.)	85	59	91	86	96	49
Turdoides j. jardinei (A. Smith)	70	72	54	54	62	45
Species/day/month	46·0	25·6	41·8	22·1	33·6	27·9
No. of counts	27	158	65	112	108	69

* Figures unreliable.

† Dr Roberts considers Mongu birds to be a new race of *zambesiana*, which I agree with him in keeping as a separate species from *leucophrys*.

Table 4. *Sample counts: monthly distribution*

Year	Total	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1939	829	—	40	57	51	88	103	19	134	123	96	43	75
1940	720	18	42	49	100	139	52	62	13	—	94	72	79
1941	457	51	31	54	100	115	83	23	—	—	—	—	—
Totals	2006	69	113	160	251	342	238	104	147	123	190	115	154

Table 5. *Sample counts: seasonal percentages of prominent species*

Species	Wet 1938–9	Dry 1939	Wet 1939–40	Dry 1940	Wet 1940–1	Dry 1941	Total
Pycnonotus tricolor	68	55	49	54	47	57	50
Streptopelia capicola	49	30	34	34	35	52	36
Dicrurus adsimilis	26	32	32	34	39	38	34
Corvus albus	30	29	31	32	35	32	32
Cinnyris talatala	21	37	34	41	21	35	31
Oriolus monacha	28	28	24	11	13	24	21
Pogoniulus chrysoconus	6	16	8	6	16	20	13
Poicephalus meyeri	1	12	7	11	10	24	11

Table 6. *Sample counts: monthly comparisons*

Species	Apr. 1940	Apr. 1941	May 1939	May 1940	May 1941
Pycnonotus tricolor	58	58	65	54	58
Streptopelia capicola	37	54	39	42	45
Dicrurus adsimilis	29	35	20	40	42
Corvus albus	34	35	18	30	29
Oriolus monacha	19	28	31	19	21
Cinnyris talatala	45	38	12	44	39

season respectively. The yellow-vented bulbul (*Pycnonotus tricolor*), white-bellied sunbird (*Cinnyris talatala*) and brown parrot (*Poicephalus meyeri*) are all more abundant in the dry season than in the rains. The cape turtle-dove (*Streptopelia capicola*), which showed a similar fluctuation at Fort Jameson, is not apparently affected in this way at Mongu, though its numbers vary quite considerably. The daily list figures add the chin-spot flycatcher (*Batis molitor*) to the birds which show such fluctuations; and though the figures for the coppery-tailed coucal (*Centropus monachus cupreicaudus*) are undoubtedly influenced by the seasonal incidence of its call, that is not the whole explanation of their variation, though it is perhaps so in the case of the black-headed bush-shrike (*Tchagra senegala rufofusca*).

There are other variations for which no explanation can be offered, such as the big drop in the numbers of the grey-headed kingfisher (*Halcyon leucocephala swainsoni*) in 1940 and 1941, with a corresponding increase in the numbers of the related striped kingfisher (*H. c. chelicuti*); the sudden advent of the kakelaar (*Phoeniculus purpureus marwitzii*) and the rufous-bellied crombec (*Sylvietta rufescens pallida*) to conspicuousness in the 1940 dry season and the 'fade-out' of the rock sparrow (*Petronia superciliaris*) in the dry weather of 1941 and of the pearl-spotted owlet (*Glaucidium perlatum*) the season before are features for which I am unable to account.

Table 7. *Prominent species on Mongu Hill: percentages*

Species	No.	Notes
Bubulcus ibis (L.)	36	10% at Kambule
Chalcomitra senegalensis gutturalis	35	—
Cinnyris talatala	42	—
Corvus albus	85	—
Dicrurus a. adsimilis	73	—
Dryoscopus cubla hamatus	31	—
Halcyon c. chelicuti	38	—
Milvus migrans tenebrosus	22	18% at Kambule
Oena capensis capensis (L.)	25	2% at Kambule
Passer griseus diffusus (Smith)	22	Not noted at Kambule
Pogoniulus chrysoconus extoni	52	—
Pycnonotus tricolor annectans	75	—
Streptopelia capicola tropica	92	—
S. s. semitorquata	31	—
Tchagra senegala rufofusca	21	—
Tchitrea perspicillata plumbeiceps	36	—
Vidua f. funerea (Tarrag.)	32	Only one record at Kambule

5. Comparative results

Beginning in October 1939, I kept daily lists of all species observed on my visits to Mongu Hill itself. Only species noted on the hill-top were recorded and not those seen at the foot. This meant that the area was a more homogeneous one than Kambule, of approximately the same size, less wooded and more densely populated. Moreover, being surrounded on three sides by open plain and the fourth by low scrub, it is cut off from the main body of woodland to the east in a way that Kambule is not.

In all, 130 lists were made, 53 in the dry season and 77 in the rains; 85 species were included. The Rauenkaier groups are: A, 113; B, 11; C, 2; D, 2; E, 2; differing from the expected formula in respect of group E, which is too small. The lists were often very short, as many visits were brief and gave few opportunities for observation. The results must therefore be treated with caution, as the more conspicuous species are disproportionately well represented.

Of the 17 species which occurred, in more than 20% of the counts 4 were in group A at Kambule and 1 was not recorded there at all. The 17 most prominent species are given in Table 8. The list differs from the Kambule list in the expected way—in the greater prominence of open-country and plains-edge forms and the lesser prominence of woodland birds. The most numerous species is the cape turtle-dove (*Streptopelia c. tropica*), followed by the pied crow (*Corvus albus*), the yellow-vented bulbul (*Pycnonotus t. annectans*) and the drongo (*Dicrurus a. adsimilis*), in that order.

Table 8. *Sample counts: comparative figures—Mongu, Fort Jameson and Mazabuka—percentages*

Species	Mongu	Fort Jameson	Mazabuka
Pycnonotus tricolor subspp.*	50	82	37
Streptopelia capicola tropica	36	34	57
Dicrurus a. adsimilis	34	10	15
Corvus albus	32	0·4	3
Pogoniulus chrysoconus extoni	13	6	—
Uraeginthus angolensis niassensis Rchw.	—	24	9
Motacilla aguimp vidua Sund.	—	39	—
Chalcomitra senegalensis gutturalis	8	23	9
Passer griseus ugandae Rchw.	—	22	—
Laniarius ferrugineus mossambicus (Rchw.)	—	13	23†
Zosterops senegalensis anderssoni Shell.	0·05	11	—
Oriolus monacha larvatus	21	11	—
Cinnyris talatala	31	—	—
Poicephalus meyeri neavei	11	—	—
Cisticola juncidis terrestris (A. Smith)	—	—	65
Urolestes m. melanoleucos (Jard.)	—	—	32
Mirafra rufocinnamomea zombae O.-Grant‡	—	0·4	28
Lamprocolius chloropterus elisabeth Stres. and L. chalybaeus sycobius Hartl.	—	1	11

* *layardi* at Fort Jameson and Mazabuka, *annectans* at Mongu. † Includes *Dryoscopus cubla hamatus*.
‡ Formerly *M. fischeri zombae*.

Turning now to a comparison of the bird fauna of Kambule with those of more distant, but more completely studied, areas than Mongu Hill, we find that at Kambule, as at Fort Jameson, the most numerous species is the yellow-vented bulbul (*Pycnonotus tricolor*), though represented by a different race in the west. The sample counts show, however, that it is a much less dominant species at Kambule than in the east. The next most numerous species at Fort Jameson, nearly as common there as the bulbul is at Mongu, is the pied wagtail (*Motacilla aguimp vidua*), which is not recorded at all at Mongu and is only found on the Zambezi itself in Barotseland. The common wagtail in the Plain is *M. capensis simplissima* Neum., which was noted three times only at Kambule, at the end nearest the Plain.

Four species occur in 30–40% of the Mongu sample counts: of these, the cape turtle-dove (*Streptopelia capicola tropica*) is no. 2 at Mongu (36% of the sample counts) and no. 3 at Fort Jameson (34%). The drongo (*Dicrurus a. adsimilis*) is third most numerous at Mongu, occurring in 34% of the counts: at Fort Jameson, it was less conspicuous. Fourth at Mongu is the pied crow (*Corvus albus*), 32%; it was also a much less conspicuous species at Fort Jameson. The fifth species is the white-bellied sunbird (*Cinnyris talatala*), which occurred in 31% of the counts; in the Eastern Province, this is a low-level species, though I once obtained it within 12 miles of Fort Jameson. No. 5 at Fort Jameson is also a sunbird, the scarlet-chested (*Chalcomitra senegalensis gutturalis*); it occurred there in 23% of the sample counts, but at Mongu only in 8%. The fourth species at Fort Jameson is the cordon-bleu (*Uraeginthus angolensis niassensis*). It was

never noted at Kambule, though it occurs on Mongu Hill. The black-headed oriole (*Oriolus monacha larvatus*) occurs in 21% of the Mongu sample counts, but only in 11% in Fort Jameson. The grey-headed sparrow (*Passer griseus ugandae*), in 19% of the Fort Jameson counts, is in the same category as the cordon-bleu in the west—it is a bird strictly confined to the edge of the main Plain and the larger inland plains and was not recorded at Kambule.* In Table 8 are the comparative figures for all species which occur in 10% or more of the sample counts at Mongu, Fort Jameson or Mazabuka. It will be noted that only five species are common to all three, though now that the trees have grown on Mazabuka station, a sixth (*Oriolus monacha*) also occurs in sample counts in all three localities, though its status at Mazabuka remains to be worked out—present evidence suggests it is a passage migrant.

I worked out some comparative figures of the way in which the species observed fall into Rauenkaier groups, with some American figures from Linsdale's papers (5, 6, 7). It was found that the chief differences are in groups A and B, the former tending to be larger in Africa and the latter in America. Groups D and E also seem to contain fewer species in temperate America than in tropical Africa. It is interesting to note that the total number of species in any one situation varies from 100 to 200, both the extremes being from America. Not all the species are resident, or even breed within the area, but the numbers are certainly high. If we exclude the species likely to be mere vagrants (i.e. group A), we are left with 39–61 species in American habitats and 31–64 in Rhodesian. The total number of macroscopic species in two American habitats farther north than the areas worked by Linsdale is 130–140 (cited by Elton (2)). No comparable figures are available for Africa, but the correspondence between the figures suggests that birds would comprise 30–40% of the total number of macroscopic species in the area.

It may be noted that the figures do not confirm an earlier suggestion of mine (13) that the 'intermediate' groups are more numerous in the Tropics than in temperate regions; but, on the contrary, that the chief differences lie in the greater percentages of the very common and the rare groups (E and A) as compared with the intermediate species.

6. NOTES ON INDIVIDUAL SPECIES

In contrast with Mazabuka and Fort Jameson, Palaearctic migrants do not play a very conspicuous part in the bird fauna of Kambule, though the swallow and the blue-cheeked bee-eater are very numerous on the Barotse Plain. None of the 11 species recorded at Kambule gets beyond Rauenkaier group A, the most numerous being the blue-cheeked bee-eater (*Merops superciliosus persicus*), recorded on 101 days; the swallow (*Hirundo r. rustica*), on 94 days; and the willow warbler (*Phylloscopus trochilus*), on 41 days. It is odd that I have no record of the white stork (*Ciconia c. ciconia* (L.)) from anywhere in the Barotse Province and that my eight Kambule records of Abdim's stork (*Sphenorhynchus abdimii* (Licht.)), an off-season migrant from the Sudan, are all of singles or small parties on passage and are the only ones I have from the Province.

Of other intra-African migrants, the most numerous are the carmine bee-eater (*Merops nubicus nubicoides* Des Murs & Puch.), which is only partially migratory in Barotseland, and the paradise flycatcher (*Tchitrea perspicillata plumbeiceps* (Rchw.)), with 163 and 144 occurrences respectively. The amethyst starling (*Cinnyricinclus leucogaster verreauxi* (Boc.)), which occurred on 138 days, is also much less of a migrant in Barotseland than

* Barotse birds are probably *P. g. diffusus* A.Sm.

it is farther east and is only absent during the rains—a time during which it is present elsewhere in the Territory. The only other migrants of importance are Levallaint's cuckoo (*Clamator cafer* (Licht.)), 120 occurrences: the black kite (*Milvus migrans parasitus* C. Grant & M. Praed), 97; and the African cuckoo (*Cuculus canorus gularis* Stephens), 80. But a word might be added about the dusky bush-lark (*Pinarocorys nigricans* (Sund.)), which seems to be a passage migrant in early May and to appear only if the grass on the station is burnt at that time.

Finally, reference should be made to the African scops owl (*Otus s. senegalensis*). My records of this species are almost entirely by ear; and the call I attribute to it is said by the Africans to be made by a lizard (probably a species of *Agama*). If so, however, the lizard, which is a common one, must only call at night and must be silent, though active and conspicuous, during the day, which seems unlikely. The question is further discussed in a recent number of *The Ostrich* (**4**). It must, however, be born in mind that the 409 times I have recorded the owl may be an exaggeration of its frequency and some of these records may be due to confusion with the lizard.

7. Summary

A direct count of the birds of 240 acres of the Barotse National School station in June 1940, gave an average of 62 birds per 100 acres, but the value of this technique is open to question. The results of sample counts and daily lists over 1100 acres of the same station are given and the most conspicuous species is the yellow-vented bulbul (*Pycnonotus tricolor*). Considerable fluctuations in a number of common species are shown by the figures. The bird fauna of Mongu is compared with that of Fort Jameson and Mazabuka and the marked differences in composition are noted. As compared with temperate America, the bird population of even these relatively 'severe' African environments contains a greater percentage of very common and of rare species and a lower percentage of moderately common species.

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THE TEN-YEAR CYCLE IN NUMBERS OF THE LYNX IN CANADA

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(With 10 Figures in the Text)

CONTENTS

1. Introduction

THE cycle in populations of *Lynx canadensis* has received wide attention from biologists on account of the regularity and great amplitude of the rhythm it has produced in the fur catches of the Hudson's Bay Company over a long period. Discussion of this periodicity has been based entirely on the total fur returns or total sales of the Company, except for a nearly complete series of fur returns for the MacKenzie River District for the years 1822–1927 (Elton, 1933). The present paper contains further material for analysis of the total fur returns into regions, derived from archives of the Hudson's Bay Company that have not previously been published.

The search for material has been in progress since 1925, and has been aided by grants at different times from the Hudson's Bay Company; New York Zoological Society; the Leverhulme Research Fellowship Trust; the Christopher Welch Trust; Oxford University; Corpus Christi College, Oxford; the Department of Scientific and Industrial Research; and the Carnegie Corporation of New York (through the Carnegie Institution of Washington). The Governor and Committee of the Hudson's Bay Company have given very full facilities for the examination of archives and the publication of material for scientific purposes. It is a pleasure to acknowledge the assistance given by many of the Company's officials. The help of the Archivist, Mr R. Leveson Gower, has been particularly valuable. We are indebted to Dr Willard E. Ireland, Archivist of British Columbia, for supplying copies of some early fur returns of the Hudson's Bay Company that are not in the latter's own collection. We also wish to thank Mrs Phoebe Jackson, who did part of the work of extracting material from the archives in London.

2. Total lynx catches of the Hudson's Bay Company

Before describing the results of regional analysis, it is necessary to clear up some confusion that has arisen about the total collections, which have been frequently used in research publications and text-books. It can be assumed that practically all the lynx

furs were brought into the posts by trappers in the same season that they were caught. But after this they might be recorded under any of three different calendar years: the year of the Outfit in which they were caught (the actual 'year of production'), the year in which the furs were rendered to headquarters, or the year in which they were sold at auction in London. Thus a collection of lynx brought into Fort Simpson in the MacKenzie River District in March 1891 would be counted in the collection of Outfit 1890 (which ran from 1 June 1890 to 31 May 1891). It would reach the headquarters of the Company in Canada and be shipped to England in the summer and autumn of 1891 (i.e. in Outfit 1891). It would normally have been sold at auction in London in March 1892 (i.e. still in Outfit 1891). This was the sale arrangement up to about 1915. In the Company's own accounting system, furs until sold were recorded by the original Outfit in which they were caught (in this case 1890), but the sales were recorded by the calendar year of the sale (in this case 1892). In the body of this paper we have converted *all* dates into the Outfit in which they were presumably caught. One has to say presumably, because there will always have been a certain number of furs that failed to reach England in the Outfit after they were caught; but these are believed not to be more than a small fraction of the total.

The Company therefore used only two of the three possible methods of dating. But those who have used the figures for scientific purposes have often made mistakes in converting the dates into 'years of production'. In order to try and clear up this confusion finally, we give below a comparative table of the different figures that have been published for the total annual lynx collections of the Hudson's Bay Company. Those in Seton (1912) and Hewitt (1921) have been read off as closely as possible from their curves, as no tables of figures are given.

Table 1. *Comparison of published Hudson's Bay Company total lynx figures, re-dated by Outfits*

	H.B. Co. (1878) moved back 2 years	Poland (1892) moved back 1 year	Seton (1912) moved back 1 year	Jones (1914) moved back 2 years	Hewitt (1921) Moved back 1 year	Hewitt (1921) Moved back 2 years
1821	—	8,986	9,000	—	9,000	—
1822	—	7,173	5,000	—	4,000	—
1823	—	6,456	4,000	—	3,000	—
1824	—	5,104	3,000	—	2,000	—
1825	—	5,161	3,000	—	3,000	—
1826	—	7,254	7,000	—	7,000	—
1827	—	11,550	10,000	—	10,000	—
1828	—	20,558	20,000	—	21,000	—
1829	—	24,611	24,000	—	25,000	—
1830	—	38,200	36,000	—	36,000	—
1831	—	16,347	14,000	—	15,000	—
1832	—	870	2,000	—	3,000	—
1833	—	14,255	15,000	—	14,000	—
1834	—	6,990	5,000	—	5,000	—
1835	—	4,440	5,000	—	5,000	—
1836	—	31,887	30,000	—	29,000	—
1837	—	45,152	45,000	—	44,000	—
1838	—	66,691	65,000	—	63,000	—
1839	—	35,843	35,000	—	35,000	—
1840	—	45,143	46,000	—	45,000	—
1841	—	10,034	10,000	—	10,000	—
1842	—	8,247	6,000	—	5,000	—
1843	—	7,173	5,000	—	6,000	—
1844	—	10,359	10,000	—	10,000	—
1845	—	21,180	20,000	—	17,000	—
1846	—	31,062	30,000	—	29,000	—

Table 1 (*continued*)

	H.B. Co. (1878) moved back 2 years	Poland (1892) moved back 1 year	Seton (1912) moved back 1 year	Jones (1914) moved back 2 years	Hewitt (1921) Moved back 1 year	Hewitt (1921) Moved back 2 years
1847	—	47,065	45,000	—	44,000	—
1848	—	43,253	40,000	43,738	41,000	—
1849	—	20,604	20,000	20,353	19,000	—
1850	—	9,303	10,000	8,519	10,000	—
1851	5,361	6,722	9,000	5,361	8,000	—
1852	4,552	4,850	6,000	4,552	7,000	—
1853	5,682	4,907	5,000	5,682	5,000	—
1854	11,358	10,764	10,000	11,358	10,000	—
1855	23,362	21,511	20,000	23,362	20,000	—
1856	31,642	32,264	30,000	31,642	30,000	31,000
1857	33,757	33,038	32,000	33,757	—	32,000
1858	23,226	27,460	25,000	23,226	—	25,000
1859	15,178	15,968	14,000	15,178	—	18,000
1860	7,272	7,927	7,000	7,272	—	11,000
1861	4,448	4,616	4,000	4,448	—	4,000
1862	4,926	4,570	4,000	4,926	—	5,000
1863	5,437	4,760	6,000	5,437	—	6,000
1864	16,498	17,044	15,000	16,498	—	16,000
1865	35,971	34,732	35,000	35,971	—	35,000
1866	76,556	68,097	65,000	76,556	—	77,000
1867	68,392	70,372	70,000	68,392	—	67,000
1868	37,447	39,119	36,000	37,447	—	40,000
1869	15,686	19,992	15,000	15,686	—	13,000
1870	7,942	8,806	6,000	7,942	—	7,000
1871	5,123	5,679	5,000	5,123	—	5,000
1872	7,106	4,839	4,000	7,106	—	9,000
1873	11,250	10,045	10,000	11,250	—	13,000
1874	18,774	17,849	15,000	18,774	—	18,000
1875	30,508	18,868	16,000	30,508	—	29,000
1876	—	43,575	40,000	42,834	—	41,000
1877	—	37,490	36,000	27,345	—	28,000
1878	—	21,291	20,000	17,834	—	17,000
1879	—	14,767	14,000	15,386	—	15,000
1880	—	10,053	10,000	9,443	—	8,000
1881	—	7,581	5,000	7,599	—	5,000
1882	—	8,016	9,000	8,061	—	8,000
1883	—	27,119	26,000	27,187	—	27,000
1884	—	51,414	50,000	51,511	—	50,000
1885	—	73,878	71,000	74,050	—	74,000
1886	—	78,555	78,000	78,773	—	78,000
1887	—	33,720	31,000	33,899	—	37,000
1888	—	18,726	17,000	18,886	—	17,000
1889	—	11,445	10,000	[11,520]	—	12,000
1890	—	—	6,000	8,352	—	7,000
1891	—	—	5,000	8,660	—	6,000
1892	—	—	10,000	12,902	—	12,000
1893	—	—	20,000	20,331	—	20,000
1894	—	—	34,000	36,853	—	36,000
1895	—	—	55,000	56,407	—	55,000
1896	—	—	38,000	39,437	—	37,000
1897	—	—	26,000	26,761	—	26,000
1898	—	—	14,000	15,185	—	15,000
1899	—	—	5,000	4,473	—	5,000
1900	—	—	9,000	5,781	—	6,000
1901	—	—	11,000	9,117	—	8,000
1902	—	—	25,000	19,267	—	18,000
1903	—	—	37,000	36,116	—	37,000
1904	—	—	55,000	58,850	—	57,000
1905	—	—	60,000	61,478	—	61,000
1906	—	—	36,000	38,501	—	32,000
1907	—	—	7,000	9,704	—	7,000
1908	—	—	—	3,410	—	2,000
1909	—	—	—	3,774	—	2,000
1910	—	—	—	—	—	6,000
1911	—	—	—	—	—	12,000
1912	—	—	—	—	—	—

The basic series for fixing the real dates of the collections is that in the Company's published report (1878) on Outfit 1876, which clearly says: 'Statement of furs and skins sold by the Hudson's Bay Company in each year, 1853 to 1877 inclusive.' The text also refers to the Spring Sales of 1877, 'when Furs of all descriptions, fine and common, were sold...'. The lynx sales figure for 1877 therefore refers to the Spring Sales of 1877, i.e. to the furs caught in Outfit 1875. These sales figures for 1853–77, that is Outfits 1851–75, overlap and agree with those given by Jones (1914). These are correctly entitled: 'Fur Sales of the Hudson's Bay Company (supplied to the High Commissioner for Canada for the Commission of Conservation).' Much the same figures appear to have been used by Hewitt, though referred to by him as 'returns', for he says: 'Through the kindness of Mr W. H. Bacon, late fur commissioner of the Hudson's Bay Company, I have been able to obtain the fur returns of that company covering a long period of years, from 1821 to 1914....From these figures the accompanying charts have been prepared.' These figures can only be brought into line with those already mentioned by assuming a mistake in transcription. For his years 1857 and 1858 he seems to have used two versions of the same figure, so that we have had to move his figures up to 1857 back by one year, and those from 1858 onwards back by two years. This gives as good an agreement as can be expected, considering that we have taken the figures from a very small diagram. Another way of describing this is that Hewitt records the first part of his series under the Outfit year of the sales, and the second part of the series under the calendar year of the sales. Elton (1924) copied Hewitt's chart, and stated that they could be converted into 'years of production' by subtracting one year. We can now see that this procedure was correct up to Outfit 1856, but wrong after that. Poland (1892) makes quite clear the situation about lag between collection and sales, and MacLulich (1937) has properly drawn attention to its importance, and suggested a correction of Elton's treatment. But Poland, though implying that his figures are London sales, has evidently dated them by the year after the Outfit of collection. This is curious, because he clearly stated: 'In the subjoined list of the Hudson's Bay Company's sales, the quantities quoted are those that are imported towards the end of the previous year, excepting those shipments which are delayed by the ice to the north of Hudson's Bay; these do not arrive till the year after. The goods from the North-west district were originally sold in the year in which they arrived, but since the September sales have been suspended, they are sold the following year. As they take much longer in the voyage than those from other districts, they have been quoted for the year in which they arrive.' Poland was dating the sales by their Outfit year instead of their calendar year, i.e. by the second of the possible methods of recording, but not one used by the Company itself. (His reference to delayed furs from the North-west clearly applies (as the earlier text proves) to those from British Columbia, which formed a small fraction of the total. His adjustment may give a slightly truer record of the real annual collection, but does not affect the general picture. We have no material for making a similar correction now.) MacLulich, by using Poland's figures as if they were in calendar sales years, therefore made a mistake in the opposite direction from that of Elton. Because Seton's curves agreed with Poland's figures, MacLulich naturally concluded that they also were sales, whereas Seton had stated: 'Through the courtesy of its officials I have secured the Company's returns for the 85 years—1821–1905 inclusive.' (On his graphs he added points also for 1906–8.)

The table gives all the figures that are available for constructing a curve for the total

lynx collections since 1821, except that the series for 1821–48 which Jones copied from Poland's book, and which are identical with the latter's, has been omitted. It can be seen that Poland, Seton and Hewitt agree substantially in the period up to 1848, for which no direct evidence is available. The differences, sometimes amounting to over two thousand skins, may be chiefly due to Poland's system of dealing with the British Columbia returns, partly also to the difficulty of plotting and then reading off accurately figures from a graph. There were also some irregularities of delivery between 1833 and 1837, which are noted by Poland. All three sources register the same peak years, though there are slight differences in the minima. From 1848 to 1911 it is best to rely upon the Hudson's Bay Company and Jones's figures. In the printed figure for Outfit 1889 in Jones there is an obvious printer's error, which we have allowed for, the last digit having dropped out of the type.

In MacLulich's curve (Fig. 16, p. 109) for lynx, where it is compared with the sunspot numbers, the figures should be moved one year forward for 1750–1906, where he uses Poland and Seton. This applies also to the varying hare figures in his paper.

Having cleared up this astonishing confusion in nomenclature and transcription, we are left with a reasonably good record of the total numbers of lynx killed in Canada by the Company's trappers every year from 1821 to 1911. To these we have added records for 1915–40 (Tables 1 and 2). Discussion of the periodicity will be deferred until § 6.

Table 2. *Total collection of lynx furs, Hudson's Bay Company, 1912–13, 1915–25;*
Dominion Bureau of Statistics, all Canada, 1919–40

Outfit	H.B. Co.	Outfit	H.B. Co.	Season	Dominion	Season	Dominion	Season	Dominion
1912	22,877	1919	1,695	1919	9,499	1927	21,369	1934	22,014
1913	30,991	1920	2,571	1920	6,509	1928	11,604	1935	22,456
1914	—	1921	4,599	1921	11,673	1929	7,621	1936	17,539
1915	13,817	1922	6,028	1922	17,317	1930	7,976	1937	10,538
1916	16,259	1923	10,682	1923	26,437	1931	8,454	1938	8,109
1917	5,606	1924	11,349	1924	29,608	1932	11,932	1939	7,473
1918	2,325	1925	16,106	1925	33,054	1933	16,799	1940	6,642
				1926	28,706				

3. REGIONAL UNITS

The ultimate unit of furs in the Hudson's Bay Company's summarized accounts is the collection at each post. But these have not often survived, at any rate in series complete enough for studying cycles. We have therefore depended mainly on the returns of fur-trade districts, containing the collections of one or more posts. For most of the districts in Central and Western Canada, long runs of figures are available since 1821. But the boundaries of these districts changed a good deal from time to time, when posts were transferred and when districts were split up or amalgamated. It was therefore necessary to choose regional units which would remain as far as possible constant over long periods of years, and this has meant in a good many cases making rather large ones, including several fur-trade districts. Our aim has been to convert, with as little inaccuracy and assumption as possible, a mosaic of administrative areas of varying size and shape into a pattern of standard biological units for expressing the fur cycle. The danger of reading figures off from the administrative districts only can be illustrated by these examples: (1) Athabasca District in 1901 was half as big again as Athabasca District in 1881; (2) Nelson River District in 1828 does not overlap at all with Nelson River District in

1911; (3) Lake Huron District in 1901 is about four times the size of Lake Huron District in 1897. In this paper we shall distinguish between *Districts* (administrative and accounting units) and *Regions* (either the same or larger groupings made by us).

The history of changes in the fur-trade districts was worked out and summarized on a chart (not published here). The main sources for 1821 86 are the Annual Minutes of Council for the Northern Department and the two-yearly Minutes of Council for the Southern Department, confirmed where possible by, and sometimes amplified from, Journals, Correspondence Books and Post Fur Returns. It must be mentioned that the lists in the Minutes of Council record decisions (taken in Canada) for the transfer and establishment of posts, and although it can be learned from subsequent post lists whether or not these arrangements did eventually take place, there is no way of checking on possible delays (without a tremendous search in the archives of individual posts), and in some cases therefore the date taken from the Minutes may be a year or so too early. The Annual Reports on Fur Trade provide lists of posts for all Districts from 1886 to 1915. Some historical material assembled by Elton (1942) for the Labrador and Ungava Districts has also been drawn upon.

The sites of most of the historic posts are known, and given on the Company's published maps. Information about many of the obscurer ones has been found in the Company's archives, and in Morton's *History of the Canadian West*. Miss Johnson, of the Hudson's Bay Company archives department, has helped us over some special points. Modern place names, although not completely reliable, have occasionally been useful. The only posts not satisfactorily located are some which were in existence for a very few years. Most of them are only mentioned once. It seems likely that these were either unsuccessful posts from the start or else winter outposts of some known post.

Our information covers the whole of Canada from 1886 to the present time. The earlier records cover British Columbia from 1825 to 1857; the Middle West provinces, and those areas of the North-west territories, the Yukon and Alaska which lay in MacKenzie River fur district, from 1821 to 1870, and from 1874 on; all Ontario, except the south-east corner, from 1822 to 1857 and in 1863, and northern Ontario in 1875; the Eastmain and Rupert's River areas of Quebec from 1822 to 1857 and in 1863 and 1875. From all this material a series of maps was compiled, with the approximate position of the districts marked on them. These are not published here, but are deposited in the Bureau of Animal Population. Although minor changes were often made in these districts, the main features of many remained unchanged over long periods. The dates chosen for the maps were decided by periods of major reorganization and are: 1828, 1848, 1875, 1881, 1897, 1901.

One handicap has been the almost complete absence of accurate maps showing the boundaries of nineteenth-century districts, which have therefore had to be fixed in relation to the network of posts in each district, and the known or probable limits of trapping activities radiating from each post at the edge of a district. We have been guided by the following principles in plotting these boundaries:

(1) Districts have always, on account of the early system of transport over canoe routes, tended to occupy water basins, or sections of them. So, where there are no other indications to go by, we have marked the line of watershed as the district boundary. This rule has settled many of the main difficulties. We have not been able to make much use of Arrowsmith's maps of the Company's fur-trade districts, because he starts with an incomplete and incorrect picture of the geography of Canada, and there is no satisfactory

way of transferring his Districts on to a modern map, where the pattern of coast and rivers is different. Where our maps differ from his, it is quite likely that he also meant to follow the line of the watershed, but had no means of knowing accurately where it was.

(2) The distribution of posts being known, a line can be drawn half-way between posts in neighbouring districts, where the watershed method is not applicable.

(3) Where the boundary crossed a river valley, a compromise has to be made between methods 1 and 2, in the light of available historical information.

(4) Some guesswork has been inevitable in the case of the outer boundaries of frontier districts. Where we have reason to be doubtful about this or any other conclusion, a broken line has been used.

It must be emphasized that the boundary is not usually a demarcation line in the same sense as a political frontier. Our only claim is that it probably gives a good indication of the area over which the natives sought for furs; but this area, even when the Company's arrangements remained unchanged, must have varied to some extent from year to year, depending (to give only a short list) on the activity of the trappers, their disposition of mind and body, and conditions (such as supplies of game for food, forest fires, winter cold or depth of snow) regulating the direction and distance of their search. There must have been some overlapping between districts, when the Indians of one locality preferred to carry their custom to some other post. In the MacKenzie River District archives, which have been rather fully extracted by us, there is a good deal of information on these topics, notably in E. Smith's description of the district in 1828, which we have drawn upon. Further historical investigation of the huge mass of archives still unanalysed should make it possible to define boundaries more accurately, and make corrections.

By grouping these districts together, many of the changes in area can be eliminated from consideration, and more or less stable regions obtained. These are shown in Figs. 1–6, and the details of their construction noted in small type below. No maps after 1901 are given: the few changes which were made between 1901 and 1914 are mentioned in the notes; and after 1915, when the returns of every post are available, we have been able to group the figures to correspond with the earlier regions.

As far as possible we have chosen for the regions titles which prevent confusion with the names of Hudson's Bay Company fur-trade districts, or with political provinces. But where the region is identical with the district through all or part of the period (MacKenzie River, James Bay), we have used the district name. Otherwise we have invented short descriptive titles. These are: Athabasca Basin, West Central, Upper Saskatchewan (i.e. River Valley), Winnipeg Basin, North Central, Lakes (i.e. Great Lakes), Gulf (of St Lawrence), West (Central, and later all British Columbia). The exact position of these can easily be seen on the maps, which give political boundaries, main rivers, and main vegetation zones, also the position of the Company's fur posts in 1927. Table 2, in § 4, shows how the available district fur returns have been grouped into these Regions.

1. *MacKenzie River Region.* This is the Hudson's Bay Company MacKenzie River District from 1821 to 1913. It covered the lower Liard, the Nelson and the MacKenzie River Basins. From 1846 to 1869 it extended into modern Alaska, with Fort Youcon on the forks of the Yukon and Porcupine rivers. At different times between 1842 and 1852 there were posts (Frances Lake, Pelly Banks, and Selkirk) in the southern section of the Yukon. The somewhat vague eastern boundary seems to have moved slowly farther east. Fort Resolution, on the south shore of Great Slave Lake, was sometimes returned under
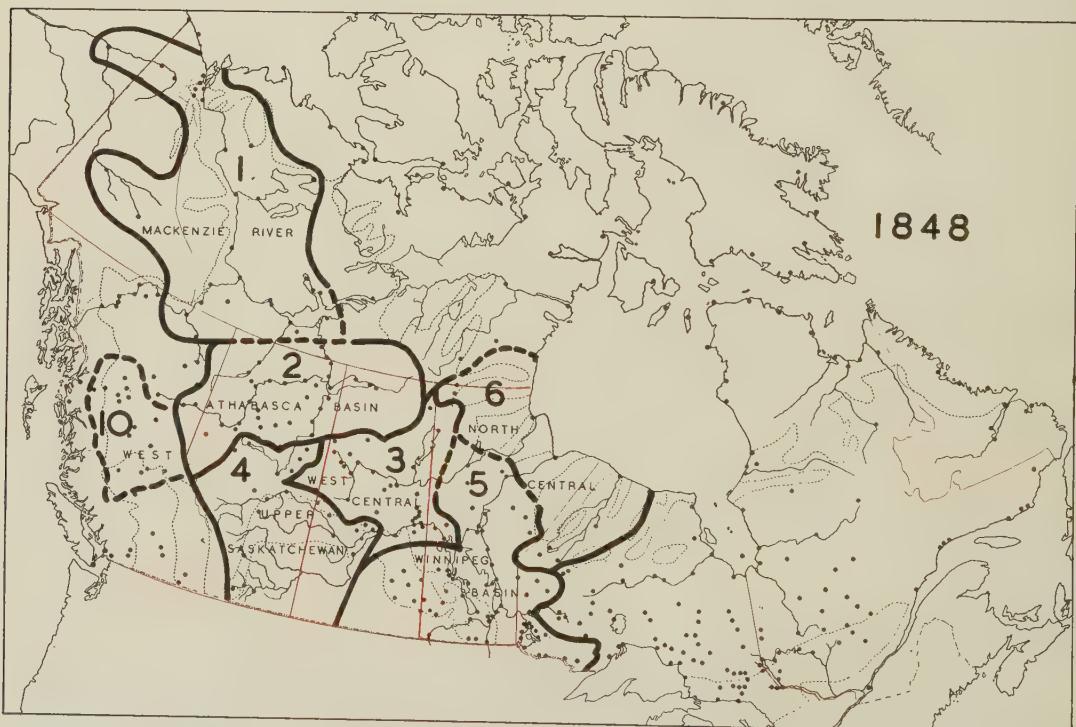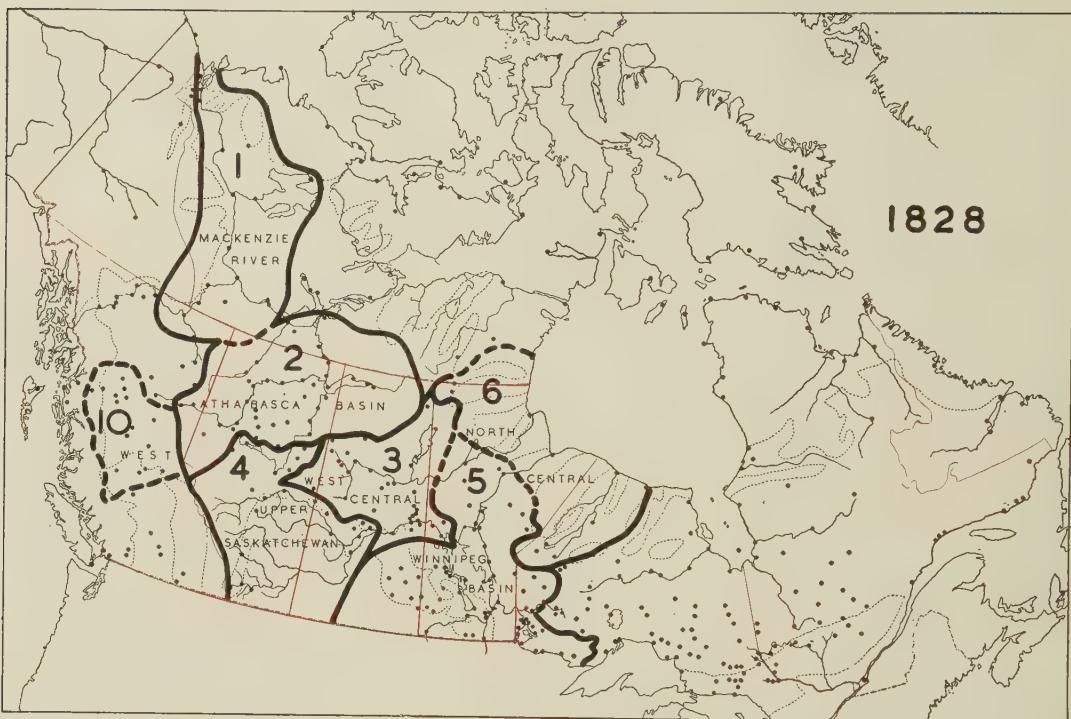
Figs. 1, 2. Regions formed by the grouping of Fur Trade Districts of the Hudson's Bay Company. Except for James Bay 1881, only those for which lynx fur returns are given have been mapped. Red lines are political boundaries. Thick broken lines are approximate region limits, where little information is available. Thin broken lines define vegetation zones. Small black dots are Hudson's Bay Company posts in 1927.
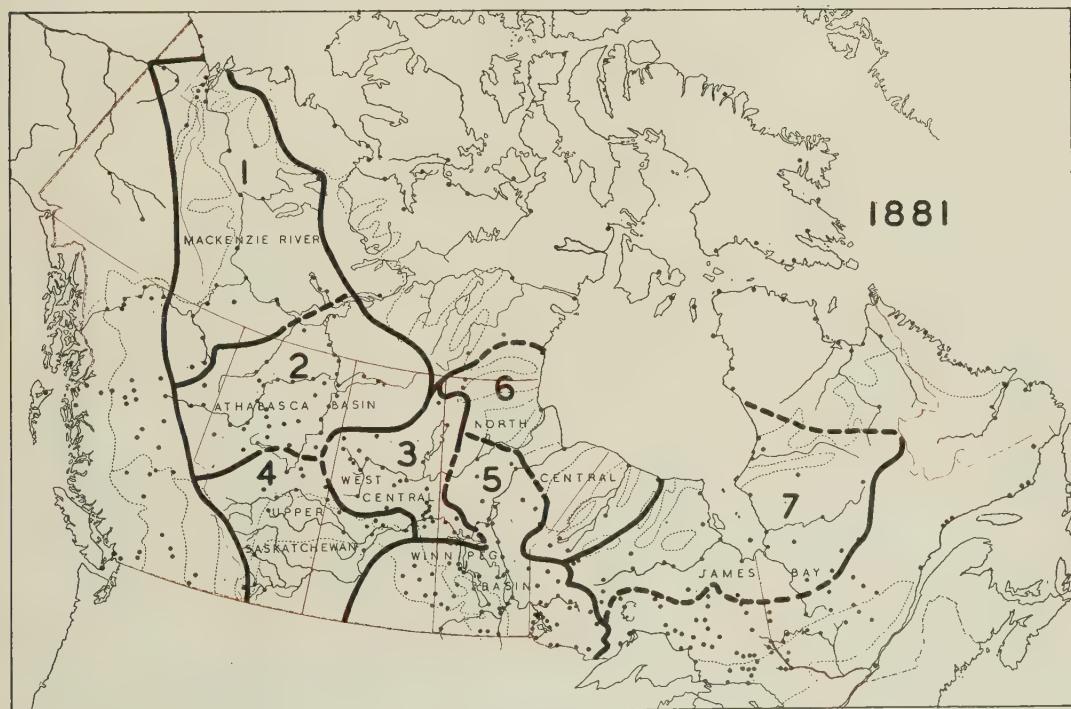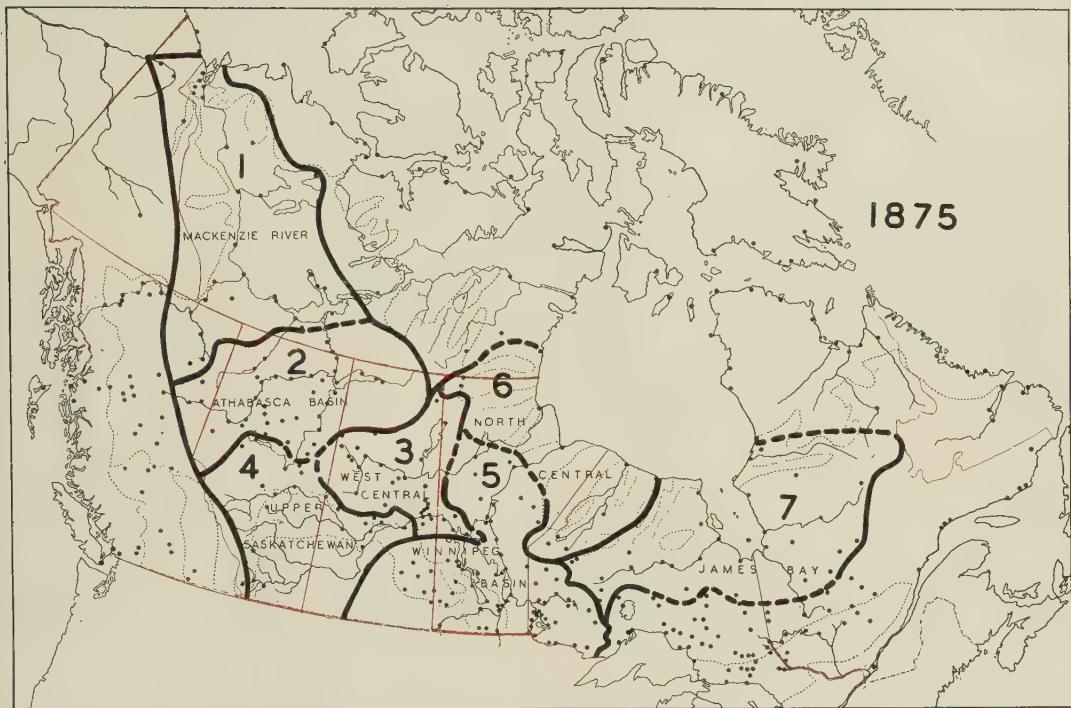
Figs. 3, 4.
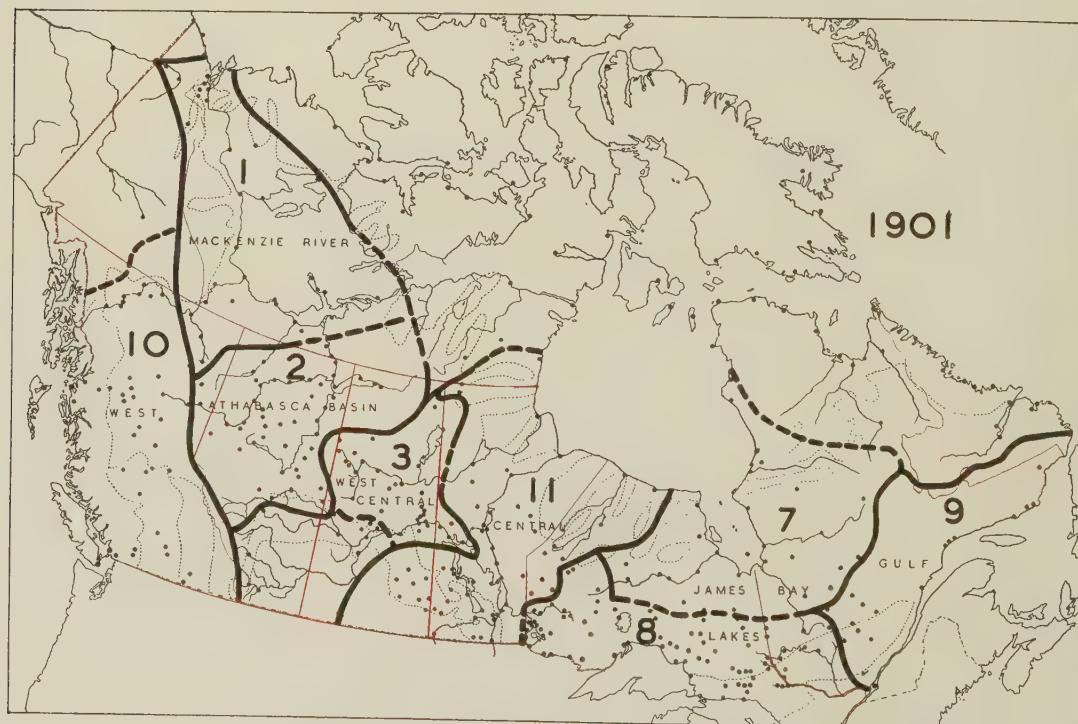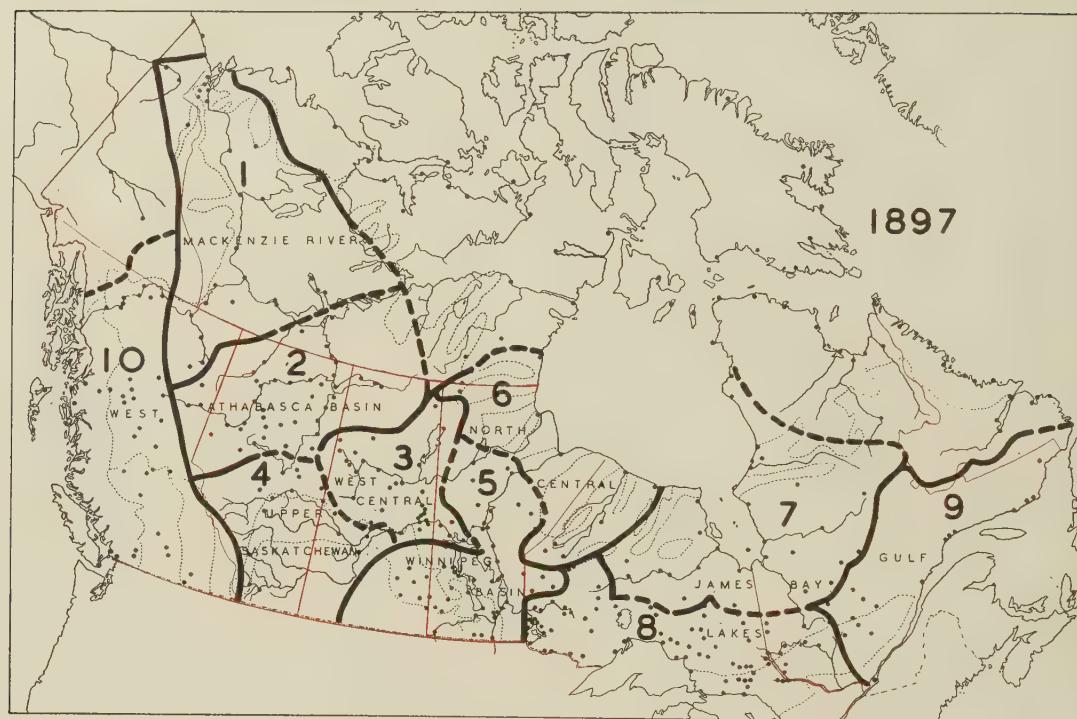
Figs. 5, 6.

MacKenzie River District (1843–78, 1899–1928), and sometimes under Athabasca District (1820–42, 1879–98).

In the grouping of the posts into older districts, in the period after 1915, we have used the map for 1901, on which, except for the transfer of Fort Smith from Athabasca District, the region was not altered until 1915.

2. *Athabasca Basin.* This region covered the Peace River Basin down from Fort St Johns and Hudsons Hope, the surroundings of Lake Athabasca, and much of the Athabasca River Basin. For the boundary between it and MacKenzie River Region, see the note above. Fort St Johns was not in operation from 1824 to 1857, which probably reduced the proportion of furs coming from the Upper Peace River. In the south the establishment of Fort MacMurray in 1871 extended the Athabasca District's trade along the upper Athabasca River; and there was further increase towards the south when the post of Lesser Slave Lake was transferred from Saskatchewan District to Peace River District in 1881. In 1899 Athabasca District was reconstituted to include Peace River and Edmonton Districts, thus extending the Athabasca Basin Region again farther into southern Alberta, as far as Onion Lake. There was a slight retraction in 1911, when Onion Lake was put back into Saskatchewan District (part of West Central Region).

For the grouping after 1915, we have used the 1901 map.

3. *West Central.* Most of this region lies in the basin of the Upper Churchill River, from Lac du Brochet and the Manitoba border on the east, to the Alberta border on the west. It also includes the lower stretch of the Saskatchewan River, from below Prince Albert down to Lake Winnipeg. In the early years the immediate north-west shore of Lake Winnipeg came under Norway House District, included in our Winnipeg Basin Region, but after the establishment of Grand Rapids post in 1865 it was in Cumberland District. The boundary with Upper Saskatchewan Region was shifted from time to time by the transfer and retransfer of Fort á la Corne, which was in Cumberland District (West Central Region) in 1853, 1857–73, and from 1892 onwards, but in Saskatchewan District (Upper Saskatchewan Region) in 1874–91. Moose Woods post, operating from 1859 to 1875, went with it.

For the grouping after 1915, we have used the 1901 map, the only transfer between 1901 and 1914 having been Onion Lake post.

4. *Upper Saskatchewan.* This covered the drainage basin of the Saskatchewan River and its tributaries as far down as Prince Albert, and for some years Fort á la Corne (see above). The series cannot be continued after 1898, when Edmonton District was incorporated in the Athabasca District, leaving no other posts in operation.

5. *Winnipeg Basin.* This rather complex grouping of districts covered the whole of the (Canadian) basin draining into Lake Winnipeg, not including the Saskatchewan River Basin, but including also the outlet of Lake Winnipeg through the upper Nelson River. The western boundary was stable, except for the smallish area on the north-west shore of Lake Winnipeg, noted under West Central Region. The boundary with North Central was stable. The area covered in Ontario varied with the development of the Lac la Pluie District. Lac Seul post was put into it from Albany District (James Bay Region) by 1870. After 1892, when Osnaburgh was similarly transferred, it seemed better to include Lac la Pluie under Lakes Region. For the four years 1897–1900 therefore Winnipeg Basin Region included no Ontario posts; only Little Grand Rapids on the Manitoba border may have received some Ontario-caught furs.

For 1901–10 no comparable series of figures is available, because of the amalgamation of Norway House and York Districts as Keewatin District. To give some indication of what was going on in the Winnipeg Basin and North Central Regions during this period, we have made a combined Central Region, which includes Keewatin, Manitoba and Winnipeg Districts, and covers roughly both regions. After 1911, when Nelson River District, which corresponds almost exactly with our North Central Region, was split off from Keewatin District, the group Keewatin-Winnipeg Districts can again be used as comparable with the earlier Winnipeg Basin Region. But it should be noted that, as in Alberta, the contribution from the south was decreasing with the settlement of the country, and that 1911 was the last year when any returns came in from the Manitoba District posts. Weenusk post was included after 1907, extending the region somewhat south along Hudson Bay.

As Winnipeg Basin does not show separately on the 1901 map, we have used the 1897 map (which also applies to 1900) as a basis for the grouping of posts after 1915.

6. *North Central.* This region covered the coastal districts of Manitoba on Hudson Bay, probably extending into what are now the North-west Territories in the north, and to the south including the Severn River Basin in Ontario, with Severn post at the mouth from 1821, and Trout Lake on its upper waters from 1834. From 1829 to 1830 inclusive, Severn post was abandoned as unprofitable; but some Indians may have made their way either to York Factory, or Island Lake (Winnipeg Basin Region). There is a gap from 1901 to 1910, discussed under Winnipeg Basin Region. The new District of Nelson River, started in 1911 (and utterly different from the old Nelson River District), covered roughly the same area as North Central. Its extension northwards by the inclusion of the new post at Chesterfield Inlet in 1911 cannot have affected the lynx collection, as this is Subarctic country.

The 1897 map has been used as basis for the grouping after 1915.

7. *James Bay.* This region covered the area draining into James Bay, except for the headwaters of rivers running from the south. It gradually extended up the Hudson Bay coast of Quebec, on which Great Whale River post was established in 1854. It became reduced in Ontario by the transfer of Lac Seul post to Lac la Pluie District some time between 1857 and 1870, and of Osnaburgh post in 1892, and Fort Hope post to Lake Superior District in 1910.

We have used the 1901 map as basis for the grouping after 1915.

8. *Lakes.* This region included all the Ontario posts not disposed of between Winnipeg Basin Region and James Bay Region, also the upper basins of the Temiscamingue and Gatineau Rivers in Quebec. The early periods, for which we have fur returns (1852–62, 1887–90), fall between the dates of our regional maps, but the component districts are listed in Table 3. The accounts gave no returns for Lake Huron District, 1857–62, and it is uncertain whether it remained in Lakes Region and was included in another district or not. (It might have gone into Montreal Department for 1857–62, but we have no material for checking this.) The region probably remained the same in 1887–90.

9. *Gulf.* From 1886 this region covered the rivers flowing into the north side of the St Lawrence from about Montreal in the west to the height of land between Natashquan River and Hamilton River in Labrador. The northern boundary did not strictly follow the watershed, as it included the headwater of the Nottaway River flowing into James Bay, and excluding Misstassiny post. Montreal Department, 1839–52, must have covered much the same area, except that it included Esquimaux Bay District on the Labrador coast. Our knowledge of adjoining districts shows that the western and north-western boundary of Montreal Department roughly corresponds with the later outline of Gulf Region. So we have used these figures, but do not show Gulf Region on the 1848 map, because we have no means of plotting the districts exactly.

10. *West.* Through the first half of the nineteenth century this region was the same as New Caledonia District, which covered the upper Skeena River, and the Fraser River and its tributaries above Fort Alexandria. For the period 1857–96 inclusive we have no fur returns and have not gone into the history of the area. From 1897 we have used a much larger area for this region, but the northern extension (which included a part of the Yukon) is the chief important addition, as the coast and southern British Columbia are not good lynx country.

4. FUR RETURNS SINCE 1821

With two exceptions, noted below, all figures from 1821 to 1913 have been obtained from the London archives of the Hudson's Bay Company; and those for 1915–39 are from detailed statements supplied by the Company's Fur Trade Department in Winnipeg. The figures for MacKenzie River Region, 1892–6 and 1914, are from a series of returns for the MacKenzie River District, 1863–1927, which was supplied to Elton in 1928 by Mr Charles French, then Fur Trade Commissioner of the Company in Canada, who said that they were obtained from private records kept by some of the older fur-trade factors. The series for New Caledonia 1825–56 is from a manuscript 'Skinbook' (now in the Provincial Library, British Columbia) kept by James Douglas, a famous chief factor of the Hudson's Bay Company. This book also gives returns, over the same period, for the posts in Columbia District. Our attention was first drawn to it through the paper by

Dr Ian McT. Cowan (1938), who kindly put us in touch with the Provincial Archivist. As will be seen in § 6, these western fur returns are of particular importance from a theoretical point of view.

Table 3. *Hudson's Bay Company fur returns: grouping of returns into regional returns*, 1821–1913

Region	Districts or Fur Purchasing Agencies
1. MacKenzie River	MacKenzie River, 1821–1914
2. Athabasca Basin	Athabasca, 1821–91, 1897–1913 Peace River, 1878–98
3. West Central	English River, 1821–91, 1897–8 Cumberland, 1821–91, 1897–1900 Saskatchewan, 1901–13 Grand Rapids, 1877–82
4. Upper Saskatchewan	Saskatchewan, 1821–91, 1897–8 Edmonton, 1874–91, 1897–8 Battleford Fur Purchasing Agency, 1897 Prince Albert Fur Purchasing Agency, 1897–8
5. Winnipeg Basin	Nelson River, 1821–36 Island Lake, Swan River, Lac la Pluie, 1821–91 Norway House, 1821–91, 1897–1900 Red River, 1821–88 Winnipeg, 1821–31, 1889–91, 1897–1900, 1911–13 Manitoba, 1875–91, 1897–1900 Lake Winnipeg, 1889–91 Keewatin, 1911–13
6. North Central	Churchill, 1821–86 York, 1821–91, 1897–1900 Severn, 1821–8, 1831–86 Trout Lake, 1834–86 Nelson River, 1911–13
7. James Bay	Albany, Ruperts River, Moose, 1852–62, 1865–75, 1895–1900 Eastmain, 1854–62, 1865–75, 1895–1900 James Bay, 1901–13
8. Lakes	Abitibi and New Brunswick, 1852–62, 1865–75, 1887–90 Kinogumissee, 1852–62, 1865–75, 1889–90 Temiscamingue, 1852–62, 1887–90, 1897–1900 Grand Lac, Pic, Long Lake, Fort William, 1852–6 Michipicoten, Nipigon, 1852–6, 1887–90 Saulte Ste Marie, 1852–62 Lake Huron, 1852–6, 1887–90, 1897–9, 1901–13 Lake Superior, 1857–65, 1897–1913 Lac la Pluie, 1897–9 Mattawa Fur Purchasing Agency, 1897–9 Rat Portage Fur Purchasing Agency, 1897–1902
9. Gulf	Montreal Department, 1839–52 St Maurice and Saguenay, 1897–1900, 1912–13 Montreal Fur Purchasing Agency, Bersimis and Mingan, 1897–1900 St Lawrence, 1901–13
10. West	New Caledonia, 1825–56, 1897–1900 Cariboo and Port Simpson, 1897–1900 Victoria Fur Purchasing Agency, 1897–1907 Kamloops Fur Purchasing Agency, 1897 British Columbia, 1901–13
11. Central	Winnipeg, 1901–2, 1905–8 Manitoba, Keewatin, 1901–10

For certain dates, independent versions of the MacKenzie River District and Athabasca District fur returns are available in the Post and District Account Books, sometimes in the form of detailed post returns, and sometimes as a District total. Since the series compiled from these sources is incomplete, it is impossible to make a systematic comparison between them and those from the Department Account Books, but they agree fairly well.

Table 4. *Lynx fur returns, Hudson's Bay Company, grouped into regions*

Northern Department

	West	Mac- Kenzie River	Atha- basca Basin	West Central	Upper Saskat- chewan	Winni- peg Basin	North Central	Total	James Bay	Lakes	Gulf
1821	—	269	62	135	276	4,059	48	4,849	—	—	—
1822	—	321	65	101	192	2,385	67	3,131	—	—	—
1823	—	585	25	128	116	2,208	68	3,130	—	—	—
1824	—	871	62	61	83	1,563	61	2,701	—	—	—
1825	171	1,475	106	66	33	872	58	2,610	—	—	—
1826	212	2,821	337	157	171	1,510	80	5,076	—	—	—
1827	737	3,928	1,295	457	256	1,572	19	7,527	—	—	—
1828	899	5,943	2,942	1,461	1,666	4,417	211	16,640	—	—	—
1829	1,238	4,950	2,338	2,650	2,863	10,271	1,030	24,103	—	—	—
1830	1,148	2,577	849	1,777	2,184	14,135	1,260	22,782	—	—	—
1831	96	523	64	894	826	6,676	439	9,422	—	—	—
1832	95	98	51	629	351	3,341	149	4,619	—	—	—
1833	170	184	23	293	150	2,436	30	3,116	—	—	—
1834	324	279	336	291	365	2,420	83	3,894	—	—	—
1835	282	409	711	411	1,132	3,034	180	6,311	—	—	—
1836	2,071	2,285	2,548	945	4,177	7,141	360	18,941	—	—	—
1837	3,491	2,685	4,453	1,830	10,008	14,168	565	34,744	—	—	—
1838	4,246	3,409	4,971	2,865	15,975	24,788	309	53,700	—	—	—
1839	2,673	1,824	1,148	4,244	9,158	23,572	584	42,256	—	—	191
1840	857	409	261	1,361	1,441	11,670	342	15,484	—	—	285
1841	127	151	27	427	116	3,033	158	3,912	—	—	312
1842	43	45	37	178	96	1,867	105	2,328	—	—	328
1843	64	68	179	206	186	2,226	70	2,935	—	—	203
1844	67	213	570	988	234	3,874	24	5,903	—	—	252
1845	223	546	1,714	3,016	1,741	7,063	33	14,113	—	—	258
1846	427	1,033	3,026	5,214	3,211	9,082	271	21,837	—	—	412
1847	443	2,129	4,365	6,378	11,705	10,610	755	35,942	—	—	485
1848	1,119	2,536	638	2,055	7,960	14,408	1,056	28,653	—	—	670
1849	1,080	957	86	775	1,075	3,823	589	7,303	—	—	723
1850	227	361	69	211	235	1,007	279	2,162	—	—	497
1851	185	377	45	77	112	649	126	1,386	—	—	242
1852	184	225	58	100	69	658	84	1,194	1,207	967	576
1853	420	360	4	178	109	852	37	1,540	1,282	824	—
1854	826	731	355	516	233	3,210	94	5,139	1,961	1,060	—
1855	1,512	1,638	633	1,347	518	8,668	258	13,062	2,889	1,865	—
1856	2,657	2,725	901	1,648	1,109	9,334	749	16,466	4,439	2,885	—
1857	—	2,871	1,154	1,349	2,088	17,144	786	25,392	4,397	3,800	—
1858	—	2,119	547	1,034	2,018	7,718	550	13,986	3,029	3,884	—
1859	—	684	154	641	2,255	4,372	364	8,470	1,803	2,969	—
1860	—	299	114	236	692	1,846	204	3,391	779	1,604	—
1861	—	236	92	93	186	992	64	1,663	447	1,093	—
1862	—	245	152	121	131	827	10	1,486	362	1,146	—
1863	—	552	307	430	165	1,385	82	2,921	—	—	—
1864	—	1,623	1,947	1,498	966	3,377	118	9,529	—	—	—
1865	—	3,311	3,511	6,138	4,185	9,743	163	27,051	1,352	—	—
1866	—	6,721	1,756	12,584	14,671	21,096	448	57,576	1,876	—	—
1867	—	4,245	1,432	7,940	11,258	23,588	1,045	49,508	2,641	—	—
1868	—	687	1,057	2,527	4,860	15,363	1,102	25,596	2,337	—	—
1869	—	255	375	1,181	1,589	4,780	420	8,600	778	—	—
1870	—	473	146	484	762	2,252	141	4,258	349	—	—
1871	—	358	125	101	366	701	61	1,712	279	—	—
1872	—	784	368	243	285	712	83	2,475	339	—	—
1873	—	1,594	930	556	819	1,834	125	5,858	482	—	—
1874	—	1,676	1,902	1,381	1,152	3,578	412	10,101	569	—	—
1875	—	2,251	3,006	4,117	8,857	7,235	282	25,748	883	—	—
1876	—	1,426	1,500	4,137	6,850	14,523	349	28,785	—	—	—
1877	—	756	810	2,856	3,865	12,126	320	20,733	—	—	—
1878	—	299	451	1,192	1,986	6,429	193	10,550	—	—	—
1879	—	201	401	788	1,370	7,072	116	9,948	—	—	—
1880	—	229	202	195	698	3,153	63	4,540	—	—	—
1881	—	469	851	214	282	1,318	84	3,218	—	—	—
1882	—	736	1,726	699	128	1,560	86	4,935	—	—	—
1883	—	2,042	5,736	3,015	1,161	3,587	110	15,651	—	—	—
1884	—	2,811	12,882	9,580	6,336	10,331	145	42,085	—	—	—

Table 4 (*continued*)

Northern Department

	West	Mac-Kenzie River	Atha-basca Basin	West Central	Upper Saskatchewan	Winni-peg Basin	North Central	Total	James Bay	Lakes	Gulf
1885	·	4,431	14,566	12,644	16,615	15,097	298	63,651	—	—	—
1886	—	2,511	5,900	10,928	15,774	26,636	933	62,682	—	—	—
1887	—	389	1,279	3,600	6,623	19,522	545	31,958	—	2,835	995
1888		73	435	731	3,153	10,399	320	15,111	—	2,956	1,151
1889	—	39	89	189	486	5,618	236	6,657	—	3,185	1,261
1890	—	49	391	137	540	2,055	85	3,257	—	2,581	710
1891	—	59	667	345	1,396	1,396	35	3,898	—	—	—
1892	—	188	—	—	—	—	—	—	—	—	—
1893	—	377	—	—	—	—	—	—	—	—	—
1894	—	1,292	—	—	—	—	—	—	—	—	—
1895	—	4,031	—	—	—	—	—	—	1,344	—	—
1896	—	3,495	—	—	—	—	—	—	2,149	—	—
1897	900	587	1,952	3,511	1,227	7,252	390	14,919	2,190	3,703	970
1898	529	105	862	959	1,183	3,399	376	6,884	1,374	2,896	1,618
1899	480	153	355	148	—	1,303	111	2,070	496	1,573	1,776
1900	618	387	612	313	—	1,172	53	2,537	371	1,453	727

Northern Department

	West	Mac-Kenzie River	Atha-basca Basin	West Central	Winni-peg Basin	Central	North Central	Total	James Bay	Lakes	Gulf
1901	709	758	1,106	1,166	—	1,518	—	4,548	373	1,159	302
1902	1,757	1,307	5,150	3,063	—	3,993	—	13,513	615	1,657	365
1903	1,729	3,465	11,629	5,255	—	6,392	—	26,741	687	1,648	729
1904	2,619	6,991	21,761	7,749	—	10,438	—	46,939	1,182	2,162	617
1905	5,540	6,313	29,832	5,297	—	12,385	—	53,827	1,441	3,313	818
1906	4,299	3,794	16,276	2,767	—	6,600	—	29,437	1,844	2,623	856
1907	1,908	1,836	2,043	1,037	—	2,532	—	7,448	701	1,922	710
1908	560	345	254	326	—	816	—	1,741	258	913	504
1909	194	382	421	554	—	545	—	1,902	183	614	258
1910	409	808	1,204	1,594	—	718	—	4,324	195	989	465
1911	648	1,388	3,091	3,267	2,257	—	64	10,067	249	1,189	657
1912	1,537	2,713	5,326	3,400	2,165	—	77	13,681	420	1,132	540
1913	1,624	3,800	8,242	4,218	2,755	—	38	19,053	940	2,009	161
1914	—	3,091	—	—	—	—	—	—	—	—	—
1915	1,790	2,985	1,813	1,118	1,188	—	479	7,583	2,771	1,471	187
1916	1,710	3,790	1,864	1,557	1,232	—	408	8,851	2,442	2,222	513
1917	731	674	652	387	542	—	232	2,487	863	1,026	475
1918	327	81	239	338	234	—	64	956	380	342	173
1919	170	80	415	420	126	—	15	1,056	112	205	108
1920	192	108	1,013	609	179	—	9	1,918	70	217	95
1921	429	229	1,892	958	404	—	91	3,574	126	254	157
1922	687	399	2,400	819	650	—	112	4,380	392	370	130
1923	1,035	1,132	3,944	1,112	1,196	—	289	7,673	623	844	388
1924	1,337	2,432	3,555	490	733	—	108	7,318	882	1,022	646
1925	1,807	3,574	3,566	792	1,168	—	159	9,259	1,148	1,881	1,476
1926	1,539	2,935	2,227	567	1,170	—	179	7,078	801	2,377	1,027
1927	1,017	1,537	1,652	356	688	—	149	4,382	378	1,428	519
1928	823	529	1,345	353	375	—	122	2,724	157	507	186
1929	363	485	1,058	285	374	—	172	2,374	86	263	159
1930	274	662	1,274	398	395	—	159	2,888	75	213	81
1931	261	1,000	1,387	254	462	—	256	3,359	180	395	157
1932	292	1,590	1,877	526	450	—	333	4,776	408	523	282
1933	425	2,657	2,391	699	569	—	504	6,821	688	577	310
1934	499	3,396	2,084	699	828	—	446	7,453	967	725	478
1935	—	—	—	—	—	—	203	—	1,291	570	566
1936	—	—	—	—	—	—	110	—	870	382	741
1937	—	—	—	—	—	—	43	—	370	221	354
1938		—	—	—	—	—	23	—	247	198	136
1939		—	—	—	—	—	37	—	149	194	111

Fig. 7. Lynx fur returns of the Northern Department, Hudson's Bay Company, 1821–1913, and of equivalent area 1915–34.

Some discrepancies, perhaps due to loss of damaged furs or errors in accounting or copying, are to be expected and do occur, but are not large enough to reverse the trend of the fluctuations, except in three cases. In two of these —MacKenzie River District, 1862 and 1866, where the Northern Department Accounts show returns of 3 and 2502 skins respectively—we have used instead the figures 245 and 6721 given in the District Account Books, which are satisfactorily confirmed by the detailed return for posts, and (1866 only) by Mr French's list. In the third case—Athabasca, 1838—we have not used the figure from the District Accounts (3831), because it is only a total, not supported by details of post returns, and because the total for the whole of the Northern Department is available for that year, and confirms the figure for Athabasca in the Department Accounts. For 1871, the Northern Department Accounts do not give any lynx for Athabasca, so we have used the total for the five Athabasca District posts, for which we have the returns for this Outfit.

The returns of the Fur Purchasing Agencies, or Saleshops, which may sometimes have handled furs from considerable distances, cannot be taken as an accurate record of local trapping. But it seems likely that the main bulk of furs traded would have come in through the centre most easily accessible, and we have therefore included agency figures in the appropriate regions, with the exception of Vancouver, which is believed to have handled Alaska furs mainly. St Johns, in Newfoundland, dealt chiefly in Labrador furs, and is omitted. Prince Albert from 1899 onward, Calgary and Saskatoon are also omitted, as they are in Upper Saskatchewan Region, for which we have no other figures after 1898 (see § 3).

The grouping of District and Fur Purchasing Agency returns into regions is shown in Table 3, and the returns themselves are in Table 4 and Figs. 7–9.

5. FUR RETURNS BEFORE 1821

A continuous record of the Hudson's Bay Company's London sales of lynx furs can be constructed, back as far as the sale year of 1736. In these early days the furs were sold at the Autumn Sales in the year they arrived, i.e. normally the Outfit after they were caught. In some years these 'Autumn Sales' included furs sold in the following January and February. Later in the eighteenth century there were also 'Spring Sales' in March. These differences have been taken into account in collating the figures, which for simplicity are described here in terms of the Outfit in which they are presumed to have been caught. There are two sources of figures, which overlap in time but show slight differences. We have extracted the original sale books for Outfits 1735–86 and 1794–9. For 1735–78 and 1786 there are 'fur marks' that record the lots from separate posts. There is also a published series of sales figures in Poland (1892), dated by him 1752–1821, obviously corresponding to Outfits 1751–1820. Both sets of figures are given in Table 5 and a composite curve in Fig. 10. The differences in most years are of the same order as those in the nineteenth-century figures, and presumably of the same nature. There is some anomaly in his year 1809, when the numbers of all species except beaver show an extraordinary drop followed by a rise to an unusual level in the following year. We conclude that either many of the furs were delayed in transit and sold a year late, or that a mistake in transcription was made.

In 1736 the Company had only six posts: Churchill River, York Factory, Severn River, Albany River, Moose River and Eastmain, all on Hudson Bay and James Bay. We

Fig. 8. Lynx fur returns of the Hudson's Bay Company, grouped into regions (West, MacKenzie River, West Central, Upper Saskatchewan, Athabasca Basin).

naturally wish to know from what area the furs were drawn, in order to be able to make comparisons with the nineteenth century and modern figures. Unfortunately, it is not easy to discover this from the historical material immediately accessible, and only a few
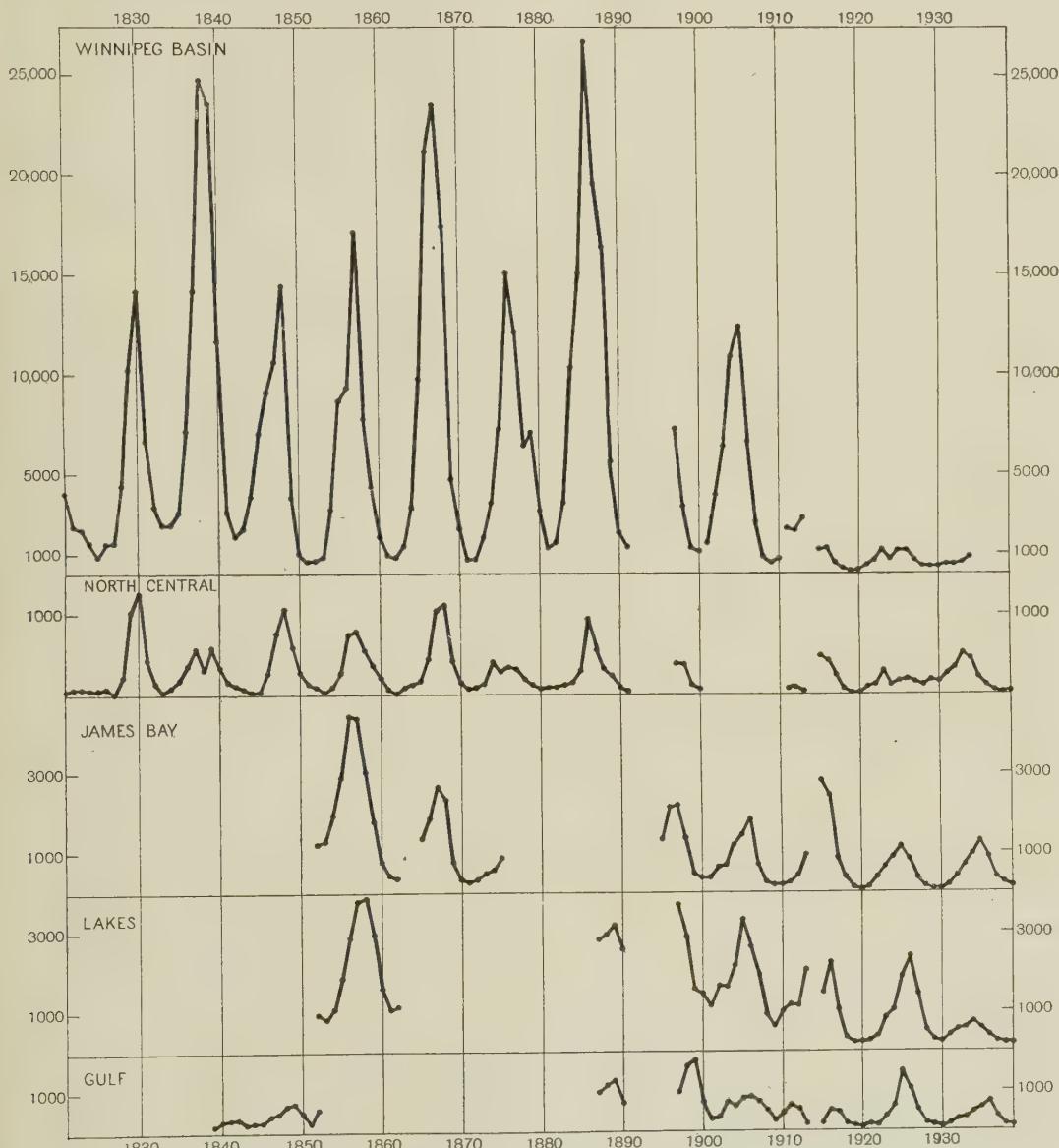
Fig. 9. Lynx fur returns of the Hudson's Bay Company, grouped into regions (Winnipeg Basin, North Central, James Bay, Lakes, Gulf).

general indications can be given, mainly based on Morton's *History* and on Innis (1930). Up to 1731 the Company had a good system of obtaining furs from inland. 'Trading Indians—with the furs of Lake of the Woods, of the valley of the Winnipeg River, and the southern basins of lakes Winnipeg and Winnipegosis —took the waterway up the

Table 5. *Hudson's Bay Company lynx sales, Outfits* 1735–1820

	Original Account Books						Poland
Outfit	Churchill River	York Factory	Albany River	Moose River	Richmond Fort	Total	(1892)
1735	97	1070	686	105	—	1958	
1736	155	989	250	70	—	1464	—
1737	80	603	387	41	—	1111	
1738	215	390	234	60	—	899	
1739	67	280	328	65	—	740	—
1740	95	457	388	50	—	990	
1741	132	761	227	44	—	1164	—
1742	344	640	85	50	—	1119	
1743	365	629	395	55	—	1444	—
1744	113	930	180	187	—	1410	—
1745	82	1027	172	118	—	1399	
1746	256	585	168	13	—	1022	—
1747	289	801	354	255	—	1699	
1748	177	911	469	203	—	1760	—
1749	507	1096	258	86	—	1947	—
1750	584	1791	380	90	1	2846	—
1751	700	3018	206	86	—	4010	4009
1752	1371	3488	370	129	1	5359	7179
1753	1378	2329	293	196	1	4197	4198
1754	553	550	116	187	4	1410	1444
1755	218	543	75	120	—	956	838
1756	225	298	7	—	—	530	631
1757	205	538	133	42	—	918	917
1758	644	733	270	89	2	1738	1881
1759	532	2246	960	104	—	3842	3842
1760	1252	2831	1070	143	—	5296	5338
1761	590	3675	1438	117	—	5820	5820
1762	1196	4164	497	160	—	6017	6000
1763	171	1754	736	231	—	2892	3005
1764	208	806	604	141	—	1759	1771
1765	175	494	377	92	—	1138	1138
1766	170	469	368	79	—	1086	1088
1767	145	638	305	41	—	1129	1128
1768	215	1904	319	69	—	2507	2508
1769	1205	2385	512	2	—	4104	4012
1770	1297	2290	708	34	—	4329	4225
1771	2311	2475	594	91	—	5471	5463
1772	624	1314	221	140	—	2299	2301
1773	956	405	263	103	—	1727	1744
1774	38	314	182	173	—	707	705
1775	88	542	285	252	—	1167	1157
1776	300	1573	379	483	—	2735	2823
1777	228	1654	389	477	—	2748	2478
1778	628	?	341	282	—	?	1245
1779	—	—	—	—	—	2619	3168
1780	—	—	—	—	—	2950	2966
1781	—	—	—	—	—	1652	1553
1782	—	—	—	—	—	980	960
1783	—	—	—	—	—	993	980
1784	—	—	—	—	—	834	822
1785	—	—	—	—	Eastmain	758	801
1786	28	577	309	137	38	1089	1080
1787	—	—	—	—	—	—	2050
1788	—	—	—	—	—	—	1550
1789	—	—	—	—	—	—	970
1790	—	—	—	—	—	—	1603
1791	—	—	—	—	—	—	1400
1792	—	—	—	—	—	—	1546
1793	—	—	—	—	—	—	989
1794	—	—	—	—	—	1092	1102
1795	—	—	—	—	—	1160	1149
1796	—	—	—	—	—	1307	1625
1797	—	—	—	—	—	1471	1541
1798	—	—	—	—	—	2878	2269
1799	—	—	—	—	—	3732	3708
1800	—	—	—	—	—	–	4495

Table 5 (*continued*)

Outfit	Poland (1892)
1801	3658
1802	2083
1803	1091
1804	820
1805	1052
1806	1588
1807	2788
1808	277
1809	7029
1810	2593
1811	1884
1812	167
1813	122
1814	131
1815	116
1816	347
1817	845
1818	1533
1819	2901
1820	4128

English River, an easterly tributary of the Winnipeg, into the Albany River and so to Albany Fort' (Morton, p. 206). Other bands went down the Nelson River to York Factory. Innis says (p. 143): 'Trade from York Factory to the interior was rapidly developed after 1713, with no competition from the French in the interior. The Assiniboines and Crees were obliged, as in Kelsey's time, to depend upon Hudson Bay for a supply of European goods, and they became middlemen trading between the Plains Indians, who had no knowledge of canoes, and the post at the mouth of the Nelson River.'

The territory tapped by the Company's posts in 1731 was therefore contained within regions 5, 6 and 7 (Winnipeg Basin, North Central and James Bay) of the 1881 map (Fig. 4), with a further extension westwards which cannot be assessed. To the south and east, the French traders still had a monopoly. After 1734, the French under La Vérendrye began a strong drive to capture the inland trade of the Hudson's Bay Company, and were partly successful for fifteen years. In 1743 the Company set up Henley House as a protective outpost of Albany inland, but Morton states (p. 228) that this was not primarily a fur-collecting post. From 1749 onwards the Company's men, under A. Henday especially, began to regain the inland trade. By 1760 the French had abandoned all their Saskatchewan posts. The extension northwards on the east side of Hudson Bay, with the establishment of Richmond Fort from 1749 to 1759, caused a temporary though relatively slight addition to the lynx catch. It was not until 1774 that the Company's inland forays to Central Canada were crystallized into a permanent trading organization by the establishment of Cumberland House on the lower Saskatchewan River. From here furs were taken down the Nelson River to York Factory. From this time onwards there was a rapid extension. This period saw the intense duplication of fur trading resulting from competition with the North-West Company, which was ended in 1820 by the amalgamation of the two concerns under the Hudson's Bay Company's name. By that date their combined trade covered all the non-Arctic regions of Canada, except for northern Quebec, the Yukon, parts of British Columbia, and the outer zones of the MacKenzie River Basin. From 1821 onwards for a number of years there was the unified
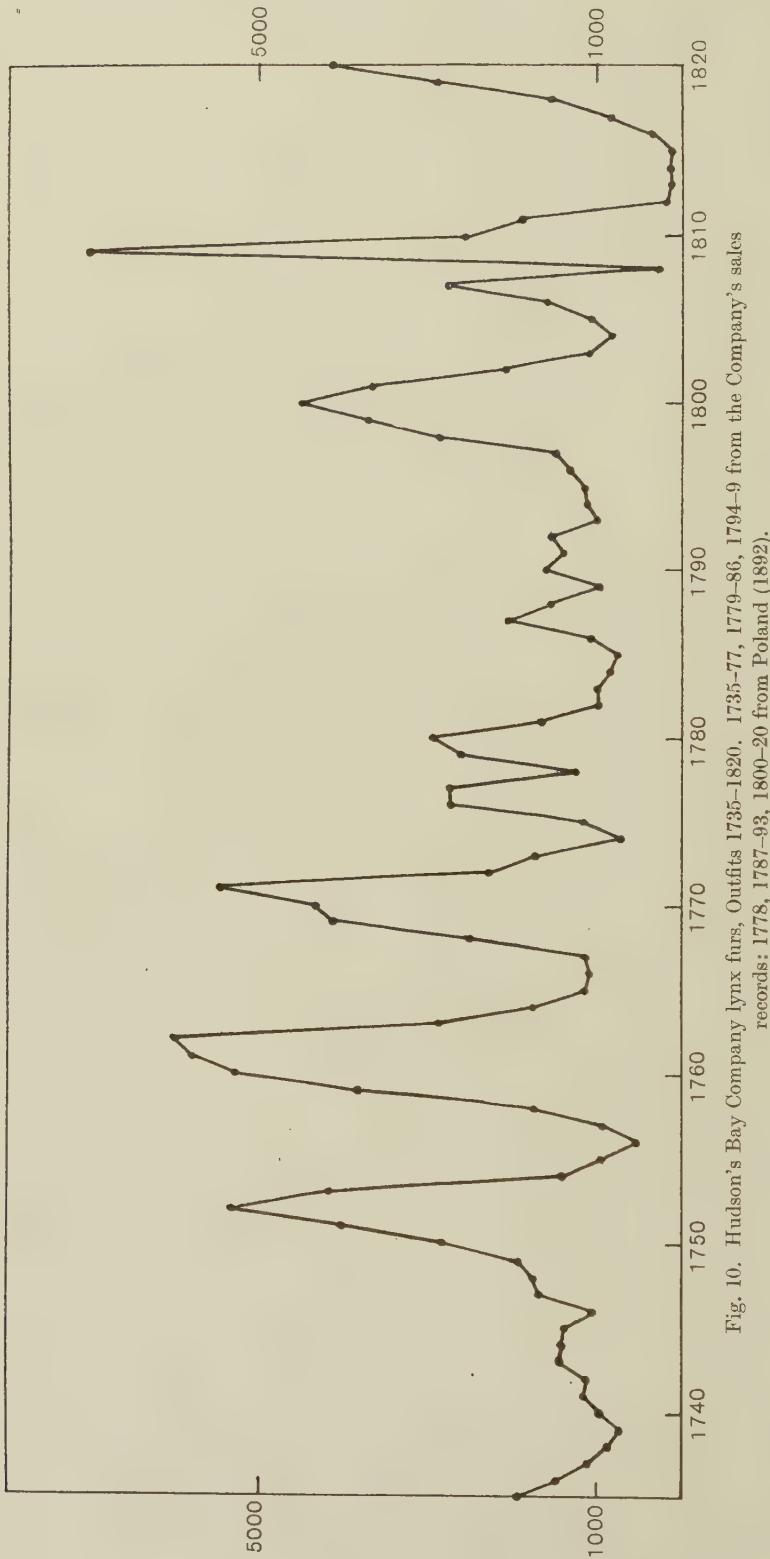
Fig. 10. Hudson's Bay Company lynx furs, Outfits 1735–1820, 1735–77, 1779–86, 1794–9 from the Company's sales records: 1778, 1787–93, 1800–20 from Poland (1892).

control of trading which gives the unique fur figures described in § 4, and this date marks a natural change in the sequence, which we have used in this analysis.

These historical notes are a necessary background for interpreting the fur figures, which were evidently subject to many changing influences, such as the irregular visits of native bands from great distances, and the trends of competition, as well as the real natural fluctuations which we are trying to detect. The main changes seem to have been the retraction of the Company's radius of influence in central Canada between 1734 and 1749, and the subsequent regaining of lost trade, and expansion to a far greater extent than before.

We have no independent check on Poland's figures for Outfits 1778, 1787–93 and 1800–20, but they are probably reliable for a general picture of fluctuations, judging by those sections of the lynx record that have been cross-checked, both before and after 1821. The anomaly in his year 1809 has already been mentioned. We have several direct bits of evidence about lynx numbers in central Canada, found in the Company's London archives, and doubtless others would be revealed by a more systematic search of the written material before 1821, which we have only investigated casually. In July 1776 Matthew Cocking recorded in the post Journal of Cumberland House, on the Saskatchewan River: 'Four or five years ago cats [lynx] were very plentiful here and in the woody parts to the Southward etc., but now the natives say there are scarce any; this is attributed to the scarcity of rabbits, these being the cats' chief food. The scarcity of rabbits was also remarked down to the northward where they used to be plentiful, owing to a supposed dearth among them.' This agrees with the high lynx catches of 1769–71, followed by a period of decrease. Peter Fidler, a remarkably keen observer who did special surveys for the Company, in his 'Report of the Manetoba District' for Outfit 1820, gives the first recorded description of the periodicity of the lynx cycle: 'There are in some seasons plenty of rabbits, this year in particular, some years very few, and what is rather remarkable, the rabbits are the most numerous when the cats appear. This winter the cats have come in considerable numbers, whereas these several years past there was scarce one to be had. Its flesh is good eating, sweet and tender, and they live principally on rabbits; the cats are only plentiful at certain periods of about every 8 or 10 years, and seldom remain in these southern parts in any number for more than two or three years. They are supposed to emigrate from the north towards the Hyperborean Sea.' He gives some further notes in his Report for 1821. The returns for lynx in the Manetoba District were: 2 in 1817 (record missing for 1818), 9 in 1819, 483 in 1820 and 883 in 1821. In this same Report he says: 'Had the martins been as plentiful as these several years there would have been a more valuable trade than would haven for these several years. . . . At Fort Dauphin House the Trade is better than last year, which is principally owing to the cats. . . . The martins this winter have been very scarce, but it is generally observed that when this happens the cats become plentiful. Four years ago there were only two cats procured in this district and had the cats not appeared, the trade would have been very little. . . .' In the Journal of Fort Dauphin (which lay on Dauphin Lake, west of Lake Manitoba), for 25 February 1820, Fidler wrote: 'The blind fellow has near a hundred cat snares down and got lately twenty cats in going once round them.' 31 October 1821: '19 rabbits. They are very plentiful this year as well as the last.'

These notes leave little doubt about the reality of the lynx peak shown in the fur returns for 1821–3. Although Fidler curiously got the relationship the wrong way round,

the correlation between lynx and rabbit abundance was realized, the phase sequence of the marten and lynx correctly stated, and the periodicity of eight to ten years remarkably close to the real average period of about 9·6, varying from 8 to 11. The statement implies a knowledge of the cycle among resident traders, that must have been the result of observation over more than one cycle, and therefore confirms the general run of Poland's figures during the previous twenty years or more. The journals of Alexander Henry (in Coues, 1897, pp. 184, 198, 221, 245, 259) contain a short series of fur returns for the Lower Red River Department of the North-West Company for 1800-5, which agree roughly with the run of the cycle shown in Poland's larger figures for the Hudson's Bay Company's whole catch:

Outfit	No. of lynx	Outfit	No. of lynx	Outfit	No. of lynx
1800	20	1802	194	1804	38
1801	67	1803	167	1805	0

The peak was 1802, compared with 1800 for the Hudson's Bay Company's total.

It will be noticed that the cycle in the Company's lynx catches, which shows up very clearly in the middle of the eighteenth-century curve, becomes rather irregular and confused between the years 1878 and 1890, though the main trend is clearly visible. There can be little doubt that this was to a great extent the result of a series of terrible pandemics of smallpox among the Indian tribes, which partly destroyed the whole basis of the interior fur trade. These epidemics have not been mentioned in the standard books on epidemiology, but Voorhis (1930) summarizes some of their dates. Although there had been earlier outbreaks in the country north of the Saskatchewan River, the culminating one advanced up the Assiniboine River in 1778 and thence spread through the West, incidentally putting a stop to the Indian wars. Between 1780 and 1783 the Lake of the Woods Region was partly depopulated and Red River and Winnipeg Regions severely affected. Hearne reported that it had destroyed nine-tenths of the Chipewyans and other northern Indians. It completely ended the fur trade in some areas for several years. Matthew Cocking, in a letter from York Factory, 12 August 1882, describes some of the disastrous effects of the smallpox on the Indians: 'Much the greatest part of the Indians whose furs have been formerly and hitherto brought to this place are now no more, have been carried off by that cruel distemper the smallpox. Mr Tomison informed me that the smallpox had destroyed most of the Indians inland, the whole tribe of Basquion Indians —their former assistants—are extinct, except one child; and that of the several tribes of Assinnee-Poets, Pigogomeu, and others bordering on Sackackiwan River, he really believed not one in fifty had survived. He said that some of the Indians who went to war last year, having met with a tent of Snake Indians who were ill of the smallpox, they killed and scalped them. By this means they received the disorder themselves and most of them died on their return. The few that reached their own parts communicated this disorder to their countrymen, and since then it has run with great rapidity through the whole country about here and is now raging among our poor Pungee deer-hunters, of whom almost every one that has been seized with it have died....Thank God we have preserved our home Indians as yet, by keeping them at a distance...' (London archives, Hudson's Bay Company).

The smallpox, killing off a large fraction of the Indian population, accounts for the greatly reduced catches of the fifteen years that followed.

6. DISCUSSION

Persistence of the cycle. The combination in series of the total sales figures for 1735–1820 with the fur returns of the Northern Department or its equivalent area for 1821–1934, gives a continuous record (except for 1914) for 200 years. The area has probably been a fairly standard one for the last 150 years, but was more limited to the westward in the first 50 years. The series demonstrates beyond any reasonable doubt the persistence of the lynx fur cycle over a large part of Canada for 200 years. The Dominion fur statistics for the whole of Canada extend the series forward for another six years. We believe that it is a rough indication of the periodicity of fluctuations of the lynx population, and it must be one of the longest homogeneous records of the sort for any species of wild animal, though there is a general historical index of changes in the Baltic herring fisheries, covering many hundreds of years. We have an unpublished record of marten furs similar to that for the lynx, but the fluctuations are not so regular, and the length of the cycle changes greatly with the shift of fur trade towards the west. Pettersson (1912) analysed the Baltic herring history and sought to correlate the different cycles with tidal periodicities affecting the entrance of saline water over the shallow entrance to the Baltic.

Although the existence of a regular historical recurrence gives no scientific guarantee of its future persistence, it can at any rate be said that the lynx cycle has so far shown no sign of dying out or changing its main rhythm. Nevertheless, there have been instances of equally pronounced fluctuations beginning and then dying out, presumably under the limiting influence of long-term changes in the ecology of the species. Elton (1924) pointed out the presence of a persistent major cycle of about 22·5 years in the irruptions of Pallas's sandgrouse (*Syrrhaptes paradoxus*) from Central Asia into the British Isles. (The dates were re-analysed by Thomson (1926), who agreed that the cycle existed.) They began suddenly in 1863, and the last big one was in 1908. But the prediction that 'we should expect another big visit about 1930' has not been fulfilled. A similar long-term cycle in rainfall has apparently affected the muskrats in the prairies of the Middle West of Canada (Elton & Nicholson, 1942).

Another factor that might change the lynx cycle is over-trapping or other human activities pulling down the whole population level to a point where no cycle could occur at all. This seems to have happened to the marten (*Martes americana*) in Canada, which used to have a major cycle of about ten years, but in recent years has diminished very greatly and no longer shows marked periodic recovery in numbers (Elton & Swynnerton, 1936).

Geographical extent. The cycle covers the whole northern forest zone of Canada, from Labrador to British Columbia and the Yukon. We have evidence also that there is a strong cycle in Alaska, though it does not always follow the Canadian one very closely. But a cycle of about ten years occurs over practically the whole range of *Lynx canadensis*.

Regional correlation. The most extraordinary feature of this cycle is that it operates sufficiently in line over several million square miles of country not to get seriously out of phase in any part of it. Table 6 brings out the remarkable degree of coherence in the cycle in regions thousands of miles apart. There are certainly differences in the peak years, and the whole Canadian peak takes several years to develop and decline. But if

the populations were operating quite independently in the various regions, such differences would in a hundred years or less have accumulated to throw them entirely out of phase. The combination of regional differences amounting to several years, with an over-all broad synchronization through eleven cycles, makes it certain that some over-riding process maintains the cycle in line over the whole extent of Canada.

It is not suggested that the regions we have chosen have any very significant ecological meaning, though they do tend to occupy river basins, whose watersheds may act as partial barriers, as shown by the presence of a separate subspecies of snowshoe rabbit *Lepus americanus macfarlani* in Alaska, Yukon and the lower MacKenzie River valley.

In reading the peak years marked in Table 6, it must be remembered that some of them differ by only a small number of skins from the year before or after. But any other method of choosing which is the peak year involves too much opinion to be safe from abuse. For the moment, we shall consider these as if they were real indices of the population peak, though this is not really the case. The peak that fell in or just before

Table 6. *Comparison of peak years (Outfits) of lynx fur returns in different regions*

West	Mac-Kenzie River	Atha-basca Basin	West Central	Upper Saskat-chewan	Winni-peg Basin	North Central	James Bay	Lakes	Gulf	Range in years of peaks
1829	1828	1828	1829	1829	1830	1830	—	—	—	3
1838	1838	1838	1839	1838	1838	1838	—	—	—	3
1848	1848	1847	1847	1847	1848	1848	—	—	1849	3
—	1857	1857	1856	1859	1857	1857	1856	1858	—	4
—	1866	1865	1866	1866	1867	1868	1867	—	—	4
—	1875	1875	1876	1875	1876	1876	1876	—	—	2
—	1885	1885	1885	1885	1886	1886	1885	(? 1889)	(? 1888)	2
—	1895	—	—	—	Central		1897	—	—	3
1905	1904	1905	1904	—	1905		1906	1905	1906	3
(1914 or 1915)	(1913, 1916)	(1913 or 1914)	(1913 or 1914)	—	(1913 or 1914)	(1914 or 1915)	(1914 or 1915)	(1913 or 1914, 1916)	(c. 1912–1916)	—
1925	1925	1923	1923	—	1923	1923	1925	1926	1925	4
—	—	—	—	—	—	—	1935	1934	1936	(3)

the war of 1914–18 cannot be defined with accuracy, partly because the figures for 1914 returns are missing except for MacKenzie River, and partly owing to the very serious disturbance of the trade with Indians that resulted from temporary variations in the Company's trading arrangements caused by market conditions at home. For this reason the probable limits within which the peaks fell are shown in brackets.

The range covered by the peak years in any one cycle has varied from two to four, the commonest number of years being three. That is to say, the peak of the lynx cycle shown in the fur returns takes several years, usually three, to develop and appear over the whole of the vast territory in which it occurs. There is no regular line of progression or geographical contouring in the incidence of peaks in different regions that can be easily seen when they are mapped in detail. But the results of a rough method of calculation suggest that there is a tendency for the peak to appear first in Athabasca Basin Region and spread west, north, south and east, and to appear last in Lakes and Gulf Regions. These figures are shown in Table 7. In each cycle the year in which the peak first appears in any region is taken as 0, the next as 1, and so on. These index figures are added up and (because the number of dates available for calculation is not the same for each region) divided by the total number of cycles for each region. The single peak for Central Region is omitted. Dates in brackets have not been used. The peak for North

Central in 1838 is taken as an average of 1837 and 1839. The Winnipeg Basin subpeak in 1926 has not been included. This broad trend from Athabasca outwards, and the late peaks in the east, confirm suggestions made to Elton some years ago by Prof. William Rowan, as a result of his studies of the snowshoe rabbit cycle in the Middle West.

Table 7

Region	Total lag in years	No. of cycles	Average lag per cycle	Region	Total lag in years	No. of cycles	Average lag per cycle
West	5	5	1·0	Winnipeg Basin	8	8	1·0
MacKenzie River	5	10	0·5	North Central	9	8	1·1
Athabasca Basin	2	9	0·2	James Bay	10	8	1·3
West Central	4	9	0·4	Lakes	6	4	1·5
Upper Saskatchewan	5	7	0·7	Gulf	8	4	2·0

Length of periodicity. Except in one or two instances where we have found substantial grounds for believing that the system of fur collection was temporarily dislocated, or mistakes had been made or records were missing (eighteenth-century smallpox, anomaly in 1808, gaps in 1892–6, war of 1914–18), it is possible to follow the cycle continuously from the middle eighteenth century. Even in years when the record was obscured, the major cycle persisted sufficiently to make any special analysis unnecessary. Such a general conclusion is made possible by the extraordinarily wide amplitude of the fluctuations. Between the peak years of 1752 and 1935 there were 19 complete cycles, giving an average period of 9·63 years. The frequency of variation around this average cannot be stated reliably from the total figures for Canada, because there is doubt as to the exact year of some of the peaks, e.g. 1809 might be 1808, 1913 might be 1914. It can be partly determined in another way, by counting all complete periods between peaks in Table 6, for the separate regions. Owing to the gaps in records for 1892–6 and 1914, the later series cannot be used except for the last cycle in James Bay, Lakes and Gulf. The result of this is to give a picture of the periodicity mainly for 1821–85. The frequency is: 1 cycle of 7 years, 6 of 8 years, 16 of 9 years, 20 of 10 years, 3 of 11 years, and 1 of 12 years. Of 47 cycles that can be measured, 36 or 78 % are 9 or 10 years. The average of the whole lot is very near that given by the total curve for a longer period, but is not directly comparable.

Relation of the lynx to the snowshoe rabbit. Although no thorough food studies have been done for the lynx, it seems to be generally agreed that its chief prey is the snowshoe rabbit or varying hare (*Lepus americanus* and subspecies), and that although it will eat other small animals and birds to some extent when it is starving, it is unable to exist successfully without snowshoe rabbit populations to prey upon. Seton (1912, ch. 14) gives some notes on the subject, remarking that 'It lives on Rabbits, follows the Rabbits, thinks Rabbits, tastes like Rabbits, increases with them, and on their failure dies of starvation in the unrabbited woods.' He describes the large numbers of lynxes roaming about in the MacKenzie River Valley in 1906–7 after the rabbits had crashed. Specimens examined contained various small rodents in their stomachs, but were starving and thin. There is not space here to review the scattered evidence on lynx food habits, but the observations of Sheldon (1930) will be cited as a particularly convincing example of the attachment of the lynx to one food. Sheldon was a first-rate field observer, who camped alone during the winter of 1907–8 on the north-east side of Mount Denali (or McKinley) in Alaska, an area now forming part of a National Park. 'In this region rabbits had been

scarce in 1906, and the year 1907 was the maximum of their periodic scarcity. Yet that year lynxes were common throughout the region...' (p. 329). A few still remained in the district that he camped in, but frequently when some rabbit tracks were seen a great horned owl would turn up almost at once, and they disappeared. Nearly all the lynxes he caught were starving. The only fat lynx seen that winter was an old female whose stomach was filled with mice and one ground squirrel—an exceptional event. 'I could discover no evidence that they were hunting mice; and mice were so abundant that if the lynxes had eaten them to any extent they must have been well fed. On the contrary all the lynxes that I examined were in a very starved condition' (p. 329). In one instance only, a lynx had killed a ewe mountain sheep weighing 130–150 lb.—presumably a rare event, as a lynx does not weigh more than about 20 lb.

Although the lynx cycle may be mainly explicable by the dependence of lynx on rabbits, it is also possible that the factor, at present unknown, which keeps the cycle in step over such large regions, may affect the lynx directly, e.g. through its rate of reproduction of physiological condition in other ways.

That the snowshoe rabbit itself has a persistent cycle averaging about 9·6 years can be shown by a large amount of evidence, part of which remains to be published.

The 206 years of lynx cycle are good evidence of the existence of a similar one in snowshoe rabbits during that period. The most promising line of research on the ten-year cycle is an intensive study of snowshoe rabbit fluctuations, recent work on which is summarized by MacLulich (1937), by Chitty & Chitty (1942) in the ninth of a series of annual reports on the cycle, and in the publications of Green and his associates (Green, Larson & Bell, 1939).

The ten-year cycle generally. The long run of figures now available proves conclusively that the hypothesis put forward by Elton (1924) of control of this cycle by sunspots, acting through climatic cycles, is not true. The 200-year record shows the short cycle getting quite out of phase with the curve for sunspot numbers, which have an average period of about 11·2, with a rather wide variation. This point has been thoroughly established by MacLulich (1937), and the hypothesis was abandoned by Elton some years ago in the light of Hudson's Bay Company records. We have at present no clue at all to the nature of the factor controlling this enormous wild-life rhythm in the northern forests, except that it seems almost certain that climatic fluctuations must play a controlling part. The cycle operates exactly parallel on both sides of the Rockies; we have unpublished notes suggesting that the introduced snowshoe rabbits on Anticosti have developed a cycle corresponding to the mainland one; the whole of Canada keeps in step without ever getting right out of phase; there is a similar cycle in the muskrat, with peaks several years before the lynx (Elton & Nicholson, 1942); also in salmon catches on the Restigouche River, New Brunswick (Phelps & Belding, 1931).

Trapping and market factors. It is frequently suggested that the cycles shown in fur returns might be caused by changes in prices acting as incentive or deterrent to the trapping of particular species. We have given reasons in our paper on the muskrat why this is not an important factor, and these reasons apply to the lynx just as strongly. In the early days, and still to a great extent, trappers brought in any valuable skin they could catch, and for long periods at a time received the same tariff rates at the posts, although in London the prices did vary inversely with the supplies sold at auction (Innis, 1927). There is also a great deal of direct evidence, both for rabbits and lynx, in the

Hudson's Bay Company Journals, etc., about fluctuations observed by trappers in the field, using evidence from tracks in the snow and other signs. The chief respect in which the fur returns fail to give an entirely reliable picture of peak years in the lynx numbers is that the predators tend to come into the traps in greater numbers when they are starving, and so there is often a lag between the real peak of rabbits and lynx, and the lynx fur peak. This subject has been discussed in relation to foxes and mice in Quebec Peninsula (Elton, 1942), and it was shown that there was sometimes no lag, but at other times a lag of a year. For the main purpose of this paper, determining the persistence and periodicity of the lynx cycle, such small differences in the peak years cannot make very much difference, though they may be of the greatest importance practically in the fur trade at a particular place and year.

7. SUMMARY

1. Hudson's Bay Company and some other records provide a record of lynx (*Lynx canadensis*) fur collections in Canada for 206 years. Details for smaller regions have been obtained for 1821–1934 or 1937. The regions have been constructed from the original fur trade districts, in such a way as to give fairly standard areas for comparing catches over long periods.

2. The cycle in lynx furs is very violent and regular and has persisted unchanged for the whole period. Its average period is about 9·6 years.

3. This cycle is a real one in lynx populations, which are dependent upon the snowshoe rabbit (*Lepus americanus*) for food, and which starve when the rabbits disappear periodically. It is therefore strong evidence of a similar cycle in snowshoe rabbits for the last 206 years.

4. The wide synchronization of the cycle in different parts of Canada for at least 100 years, its parallel occurrence both west and east of the Rockies, and its independent occurrence in aquatic species such as the muskrat (*Ondatra zibethica*) and the salmon (*Salmo salar*), strongly suggest the existence of a climatic factor partly controlling it.

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MORPHOMETRIC DATA FOR WINDERMERE

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INTRODUCTION

ECOLOGY often demands exact measurement, especially where the physical environment is concerned, and therefore in 1937 the Freshwater Biological Association decided that a detailed bathymetric survey of Windermere, conducted by modern methods, was desirable as a background for studies of the water and its biology. The original survey of the depth of the lake by H. R. Mill (1895) had provided a most useful map, but time was limited in Mill's work, all of which had to be done with a row boat and sounding lead, so that much detail was necessarily omitted. Accordingly the Hydrographer to the Admiralty was approached, and he generously allocated one of his survey officers, Lt.-Commander W. J. Farquharson, who had served previously as navigator and hydrographer on the John Murray Expedition to the Indian Ocean, together with a Petty Officer as assistant, to survey Windermere. The field work, based on Wray Castle, occupied 5 weeks in June and July 1937. The instrument used was a magneto-striction echo-sounding recorder manufactured by Messrs Henry Hughes and Son, Ltd., fitted to the Association's research launch. In this instrument a supersonic sound impulse is emitted at intervals, and the time taken for the echo to return to the surface is recorded on a continuous chart with an appropriate depth scale. The advantage over older methods is shown by the fact that it was possible within a few weeks to complete nearly 300 cross-sections on Windermere with continuous soundings, the distance between sections being about 60 yards. For each section the launch was driven at constant speed on a fixed bearing by G. Thompson, the Association's laboratory steward, while Farquharson and his assistant operated the instrument and fixed positions at intervals by simultaneous sextant readings. The results were subsequently plotted and printed by the Admiralty on Ordnance-Survey charts on the scale of 6 in. to 1 mile, depth contours being inserted at 2, 5, 10 m., and so on at 5 m. intervals. The full details are available to workers at Wray Castle as also are working maps of the lake showing depth contours only. In addition some littoral regions of the lake in the neighbourhood of Wray Castle and the Brathay Delta were surveyed in still greater detail, the results being plotted on the scale of 25 in. to the mile.

The morphometric data for the lake set out in the Table have been computed by Mortimer from Lt.-Commander Farquharson's 6 in. to the mile chart. They have already been used in a variety of work and are now placed on record for permanent reference. The measurements involved were made by W. H. Moore, laboratory assistant at Wray Castle, under Mortimer's supervision.

LAKE LEVEL AND GAUGE POINTS

The mean lake level now recognized is 129·0 ft. (39·3 m.) above Ordnance Datum. It is indicated by a bench mark in Wray Castle boat-house, and all results given below are reduced to this level. The rise and fall, which has a range of about 6 ft. has been recorded

by daily readings on a gauge in Wray Castle boat-house since January 1933, and continuously by a recording float-gauge in the boat-house since May 1938. Another recording float-gauge is maintained by the Lancashire County Council at Newby Bridge on the River Leven, the out-flow to the lake, and gauge posts for daily observations when required are established at Newby Bridge, Lakeside, and on the four main tributaries. The variations in lake level compared with rainfall, run off and storage are discussed by Capt. W. N. McClean (1940).

THE TWO BASINS

Windermere is divided into two distinct basins roughly equal in length, data being given in the Table for each separately and for the whole lake. The division between the two, where the depth of water is less than 5 m., is in the neighbourhood of Belle Isle, and for the purpose of the computations, is taken as a straight line from Cockshot Point on the east shore just south of Bowness, across Belle Isle, passing mid-way between the two

Morphometric data for Windermere. Figures in brackets are percentages

Contour m.	Area enclosed by contour sq.km.*			Layer m.	Volume of layer million cu.m.‡		
	North basin	South basin	Whole lake		North basin	South basin	Whole lake
0	8·16 (100)	6·66 (100)	14·82 (100)	0– 2	15·3 (7·2)	12·3 (10·5)	27·6 (8·4)
2	7·11 (87)	5·69 (85)	12·80 (86)	2– 5	20·0 (9·4)	15·9 (13·5)	35·9 (10·9)
5	6·21 (76)	4·90 (74)	11·11 (75)	5–10	29·3 (13·8)	22·2 (18·8)	51·5 (15·6)
10	5·50 (67)	3·99 (60)	9·49 (64)	10–15	26·1 (12·3)	17·9 (15·2)	44·0 (13·3)
15	4·95 (61)	3·17 (48)	8·12 (55)	15–20	23·5 (11·1)	14·7 (12·5)	38·2 (11·6)
20	4·45 (55)	2·72 (41)	7·17 (48)	20–25	20·8 (9·8)	12·7 (10·8)	33·5 (10·1)
25	3·88 (48)	2·36 (35)	6·24 (42)	25–30	18·2 (8·6)	10·4 (8·8)	28·6 (8·7)
30	3·40 (42)	1·81 (27)	5·21 (35)	30–35	16·0 (7·6)	7·50 (6·4)	23·5 (7·1)
35	3·00 (37)	1·19 (18)	4·19 (28)	35–40	14·0 (6·6)	3·60 (3·1)	17·6 (5·3)
40	2·60 (32)	0·25 (3·8)	2·85 (19)	40–45	11·3 (5·3)	†0·50 (0·4)	11·8 (3·6)
45	1·92 (24)	—	1·92 (13)	45–50	7·88 (3·7)	—	7·88 (2·4)
50	1·23 (15)	—	1·23 (8·3)	50–55	5·20 (2·5)	—	5·20 (1·6)
55	0·85 (10)	—	0·85 (5·7)	55–60	3·25 (1·5)	—	3·25 (1·0)
60	0·45 (5·5)	—	0·45 (3·0)	60–65	1·32 (0·6)	—	1·32 (0·4)
65	0·08 (1·0)	—	0·08 (0·5)	65–67	0·08 (0·04)	—	0·08 (0·02)
				Totals	212 (100·0)	118 (100·0)	330 (100·0)

* ×0·384 = sq. mile.   † 40–44 m.   ‡ ×220 = million gal.; ×35·2 = million cu.ft.

Lilies of the Valley Islands, and projected onwards to the west shore. The maximum depth of the north basin is 67 m., of the south basin 44 m. The mean depths are computed to be 26·0 and 17·7 m. respectively, and that of the lake as a whole to be 22·3 m. The surface area and total volume of the north basin is 55 and 64 % respectively of that of the whole lake.

PROCEDURE IN COMPUTATION

The areas enclosed by depth contours drawn on Lt.-Commander Farquharson's map were determined as an average of two planimeter measurements. The volume of water in a layer between two contours is taken to be the mean of the areas enclosed by the two contours multiplied by the thickness of the layer. The total volume was obtained by summation of such layers. One square inch on the 6 in. to the mile scale equals 0·0722 sq. km. of actual area.

ASSESSMENT OF ACCURACY

Possible errors are involved in the following:

1. Measuring water depths from echo-records. If it is assumed that the machine is recording accurately, the mean error in reading the records at all depths may be taken to

Photo C. H. Wood, Bradford
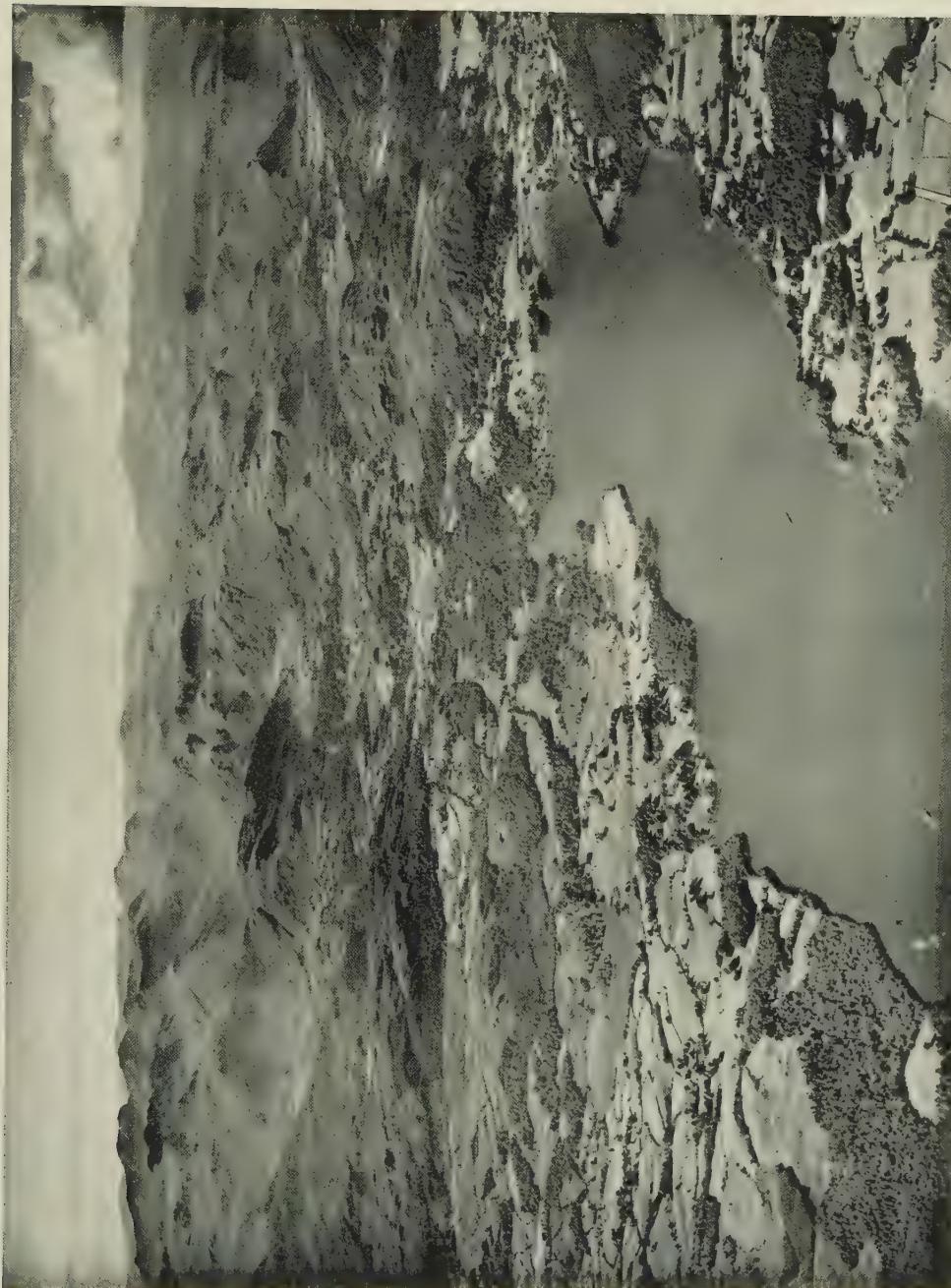
Photo 1. North end of Windermere, looking north-west. The low-lying land in the foreground is composed of Bannisdale slates, the mountains behind mainly of Borrowdale volcanic rocks. Blelham Tarn at left; Little Langdale with Elterwater in left background; Great Langdale in centre background; Rydal Water and Grasmere in right background.

be that involved in a reading at average lake depth. As readings can be made to the nearest 0·3 m., this involves an error of 1·5–2%.

2. Measuring areas on map with planimeter. Results are reproducible to within 1%.

3. Personal errors in obtaining and plotting two 'simultaneous' sextant bearings.

4. Plotting contours over areas not covered by lines of soundings.

5. The assumption, implicit in the method of computing volumes, that there is a uniform rate of decrease of area, with increasing depth, between one contour and the next.

It is difficult to assess the errors involved in 3, 4 and 5 and it is probable that many errors may balance each other out over a large area. It is estimated that the computed volumes are within 5% of the true value, so the results are expressed to three figures, the significance of the last being doubtful. Calculations have been made by slide rule, this being adequate for accuracy of this order.

Comparison with H. R. Mill's results

Mill (1895) gives the volume of Windermere as 347 million cu.m., the area as 14·79 sq.km. and the mean depth as 23·8 m. In view of the time and equipment at Mill's disposal the agreement with the data given here is very good (volume, 330 million cu.m.; area, 14·82 sq.km. and mean depth 22·3 m.). His calculations were made for a higher lake level, 129·7 to 130·0 ft. above Ordnance Datum. About 5 million cu.m. may therefore be deducted from Mill's figure for volume to reduce it to the 129·00 ft. level. This corrected value is only 4% above that given in the Table.

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SEASONAL CHANGES IN THE TEMPERATURE OF WINDERMERE (ENGLISH LAKE DISTRICT)

By PENELOPE M. JENKIN, *Department of Zoology, Bristol University*

(*With* 6 *Figures in the Text*)

CONTENTS

1. INTRODUCTION

WHEN the laboratory of the Freshwater Biological Association of the British Empire was opened at Wray Castle, on the shores of Windermere, a routine survey of the physical and chemical conditions in the lake was one of the first pieces of work to be undertaken. This survey included the measurement of water temperatures at seven or eight depths in the lake at monthly intervals from November 1931 to October 1932. The results are now recorded and made the basis for a comparative discussion of lake typology.

The writer has pleasure in expressing her long-standing debts of gratitude to the Freshwater Biological Association for affording her all the necessary facilities for carrying out the survey from their laboratory, including the use of their specially equipped motor launch; to Girton College, Cambridge, for a maintenance grant from the Alfred Yarrow Research Fund; and to Bristol University for the use of their table at Wray Castle during the preparation of this report. She also wishes to thank Mr H. Freke for drawing the map in Fig. 1, and Drs E. B. Worthington and C. H. Mortimer not only for the needful stimulus to write the report, and for their helpful criticisms, but also and more especially for Dr Mortimer's computation of lake volumes (Mortimer & Worthington, 1942, p. 245), without which the conclusions presented in this report might never have been reached.

2. THE LAKE

The English Lake District lies at about 54° 20′ N. and 31° W. close to the north-west coast of England, and bordering on the Irish Sea. It is a small mountainous region, composed essentially of a central mass of old volcanic rocks and slates, surrounded by Coal Measures and New Red Sandstone (Marr, 1916, pp. 2 et seq.), with the lakes radiating from the centre (Mill, 1895, p. 48). Windermere is the largest of the lakes and lies in the south-easterly part of the district. It shows evidence, like most of the others, of a glacial

origin; for it lies in a rock basin formed by ice erosion and has had its level raised by a glacial accumulation damming the south end (Marr, 1916, p. 176).

The *drainage basin* of Windermere occupies an area of 230·5 sq. km. Pearsall (1921 a, p. 263) estimated that 29·4 % of this basin could come under cultivation. The rocks exposed in the northern part of the basin are Ordovician, and almost entirely volcanic in origin, and are drained by the rivers Rothay and Brathay, which enter the lake by a common delta at the north end. These rivers receive respectively 28·4 and 29·7 % of the total rainfall of the basin (McClean, 1940, p. 346) and may carry silt and leaves, but only a very poor supply of electrolytes, into the lake. The only calcareous rocks in the basin occur in a relatively thin succession of impure (Coniston) limestone, calcareous shales, and mudstones which mark the summit of the Ordovician. These cross the basin near the head of the lake (map, Fig. 1), but affect very little of the inflowing water. The rocks exposed in the southern part of the basin are Silurian, beginning with a rusty-weathering blue-black (Stockdale) shale, not differentiated on the map from the Coniston limestone, and followed farther south by several thousand metres of other sediments such as flags, grits and slates. A number of less important streams drain this part of the basin, the largest being Trout Beck, which only receives 9·6 % of the total rainfall. The mean annual rainfall in the drainage basin is given by McClean (1940, p. 346) as 86·98 in. (2209 mm.) p.a., the extremes in different places being 111·4 and 66·7 in. McClean estimates (1940, p. 348), from the run-off in the River Leven, that about 30 % of the rainfall is lost by evaporation and other causes before leaving the lake.

The *present lake* stands at an altitude of 39·3 m. above sea-level. It is long and narrow, with a maximum width of less than 1·5 km. and an average width of only 0·87 km. The axis is slightly curved, running south-south-east for about 5 km. from the northern end, and then turning south. A bathymetrical survey of the lake was made by Mill (1895, pp. 155–62 and map p. 204). In 1937 a detailed echo-sounding survey was made by the Admiralty for the Freshwater Biological Association, to whom I am indebted for the results used in the construction of the map (Fig. 1). The mean depth of the lake was estimated as 23·8 m. in 1895, and 22·3 m. in 1937 (Mortimer & Worthington, 1942, p. 246). The volume appears, from this, to have been reduced by some 4 % by silting in the interval; but the accuracy of the earlier survey is probably not sufficient for the two figures to be strictly comparable. Most of the shore is covered by trees or fields. Pearsall (1921 a, p. 263), in an important discussion of the silting and possible limnological 'evolution' of the English Lakes, estimated that only about 28 % of the shore line of Windermere was still rocky to a depth of 9·2 m. (30 ft.); elsewhere the shores are stony, where they are exposed, but covered by silt in the sheltered bays as well as in deep water. Submerged and emergent aquatic vegetation has invaded some of the silted regions, such as the deltas of the River Brathay and Blelham Beck (from Blelham Tarn), as well as the shallow water round some of the islands (Pearsall, 1921 b, p. 187). The shore topography has been mapped and discussed in detail by Hay (1930, p. 328).

The lake is clearly divided opposite Bowness into north and south basins by a region nowhere more than 4 m. deep and dotted with islands, of which Belle Isle is the largest (map, Fig. 1). The *north basin*, with the Brathay delta, is comparatively simple in shape, with a few minor bays. Most of the routine survey in 1931–2 was carried out in the northern part of this basin, near to the deepest place in the whole lake. The *south basin* is longer, narrower and shallower than the north, and tapers to the River Leven, which

WINDERMERE

Coniston Limestone
and Stockdale Shales

Contours at 50 metre intervals

Soundings in metres, at
10, 30, 50 and 60 metres

Scale of Statute Miles

Fig. 1.
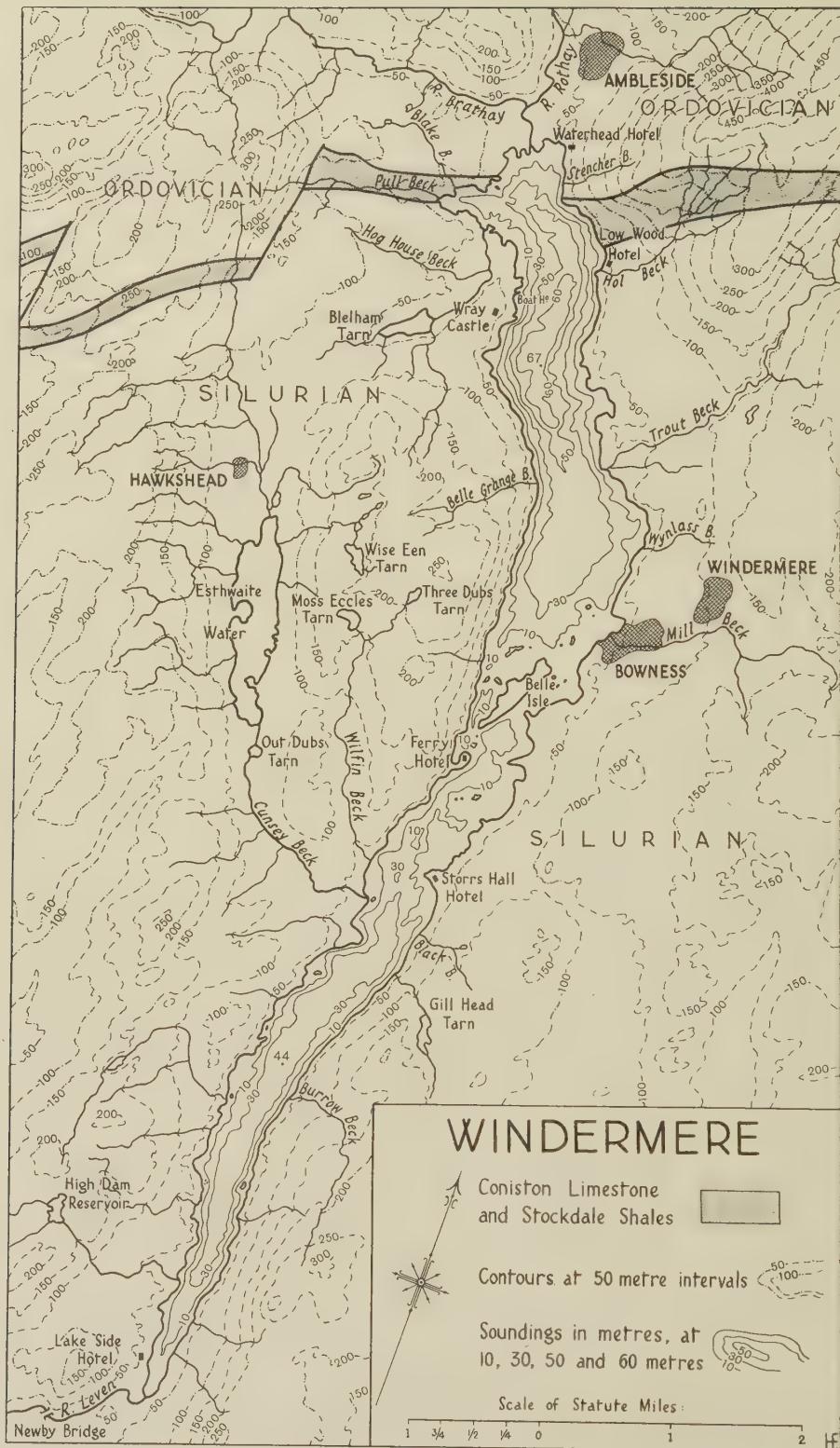
drains it from the south end. A station near the deepest part of this basin was examined in February and August 1932.

It is significant, from the limnological point of view, that the treated sewage from Ambleside (population 2000, plus as many more summer visitors) is discharged directly into the River Rothay and thence into the north basin; and that the sewage effluent from Windermere and Bowness (population 6000, plus visitors), after receiving an up-to-date treatment, is discharged into the south basin of the lake. Although this latter effluent does not contain much oxidizable matter, it adds considerably to the supply of nitrates and phosphates in the water.

Morphometrical data for Windermere

	Whole lake	North basin	South basin
Length in km.	17·0	6·5	10·5
Surface area in km.^{2}	14·82	8·16	6·66
Volume in m.$^3 \times 10^6$	330	212	118
Maximum depth in metres	67	67	44
Mean depth in metres	22·3	26·0	17·7
Length of shore line in km.	46·12	—	—
Development of shore line (length/circumference of circle of same area)	3·38	—	—

3. METHODS AND TREATMENT OF DATA

(a) *Sampling stations.* At the time of the temperature survey no fixed buoy might be left out in the lake. The sampling station in the north basin had therefore to be identified by shore marks before anchoring the boat: it lay roughly south-east of Wray Castle, near to the deepest water in the middle of the basin (Fig. 1). The actual depth encountered varied with the exact position from 55·5 to 63 m. Samples were collected on 21 occasions at either fortnightly or monthly intervals between November 1931 and October 1932, the dates being shown at the foot of Fig. 2. The station in the south basin lay north-west of the mouth of Burrow Beck, near the middle of the basin, where the depth encountered was 36–39·5 m. Samples from this basin were collected on 20 February and 31 August 1932.

(b) *Sampling routine.* The temperature of the water was measured in a closing water bottle, as soon as the bottle was brought to the surface, after having been lowered to 0·5 m. below the required depth, left for 2 min. to take up the temperature of the surrounding water, raised 0·5 m. to enclose a fresh body of water, closed and raised to the surface. The routine consisted in taking seven or eight such samples on each occasion, one at the surface, others at 10 m. intervals down to the bottom and then samples at 2 and 0·5 m. above the bottom. In the summer further samples were taken from 5 m. and occasionally from 15 m. below the surface.

(c) *Apparatus.* The closing water bottle was unusually large, having a capacity of about 7 l. It was made of tinned iron, well lagged with rope outside, with doors at

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Legend for Fig. 1.

Fig. 1. Map of Windermere, showing the lake and the southern part of the drainage basin, but omitting the sources of the River Rothay, which enters the lake via Grasmere and Rydal Water, and those of the River Brathay and Langdale Beck, the last of which flows through Elterwater. Belle Isle marks the division between the *north* and *south basins* of the lake. (Drawn by Mr H. Freke, using the Ordnance Survey map for contours and the Admiralty Echo-sounding survey of 1937 for soundings. 1 statute mile = 1·6 km.)

either end that closed on hinges and were of nearly the same diameter as the bottle. Comparisons, made on 27 July 1932 between this bottle and a standard Friedinger closing bottle, showed that the temperatures measured in the larger bottle were the more consistent, and in the case of samples from the bottom, the lower. There was no other means available for checking the results; but it was thought that this comparison showed the apparatus and method to be reasonably satisfactory. Prior to this there had been a period between 21 April and 22 July when the upper door of the bottle became loosened and sometimes allowed of contamination of the contents with water from other layers. This leakage was effectively prevented by affixing a safety catch to the door before the above comparisons were made. Any leakage was usually apparent from the results, but for safety all samples (except two with maximal values) taken from below the surface between 21 April and 22 July have been discarded.

(d) *Terminology of thermal stratification.* The classic definitions* of 'epilimnion' and 'thermocline', based as they are upon conditions in continental lakes, are not always applicable to the upper waters of Windermere during the summer stratification. Ullyott & Holmes (1936, p. 971) showed on one occasion that the upper waters of Windermere were changed, by a few days of wind, from a nameless calm-weather condition with an even temperature gradient between the surface and 17 m. to the classic condition with an epilimnion of uniform temperature from 0–13 m. and a true thermocline from 13–15 m. Possibly in continental lakes, where the range of temperature is higher, the stability greater and the weather less variable, such changes in the stratification may be less marked; but the dependence of even a typical thermocline upon wind was early noticed by Birge (1910, p. 997), although he gave no name to the upper layer in the calm-weather condition.

In the present paper, dealing with a coastal lake, the term 'Epilimnion' is extended to include this nameless condition and so to cover the warm upper layers of the lake throughout the stratification period, whatever their temperature may be. The term 'Discontinuity Layer' is revived to cover the layer of very variable thickness in which there is a sufficient temperature gradient to impede mixing of the epilimnion with the cool hypolimnion below. The classic thermocline, with its very steep temperature gradient, then becomes a special type of discontinuity layer, rather than a synonym for all such layers, as has often been assumed. This accords with Wedderburn's (1910, p. 118) original use of the term discontinuity layer in connexion with the coastal lochs of Scotland. In Loch Garry, for instance, the fall in temperature in the discontinuity layer was only 0·28° C. per m., but Wedderburn recognized that this gradient was yet sufficient to cause a definite discontinuity in the circulation of the water within the lake.

(e) *Calculation of heat budgets.* Birge (1915, p. 167) defined the 'Annual Heat Budget' of a lake as 'the amount of heat necessary to raise its water from the minimum temperature of winter to the maximum summer temperature' and the 'Summer Heat Income' as that 'necessary to raise it from 4° C.' Either was to be expressed in terms of the 'total number of calories necessary to warm a column of water of unit base (1 cm.²) and a height equal to the *mean depth* of the lake' (Birge, 1915, p. 170). The budget for each 10 m. layer (Münster-Strøm, 1931 b, pp. 496, 507) is the number of calories necessary

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* Birge & Juday (1914, p. 547): Epilimnion, 'the uppermost layer of nearly uniform temperature'; thermocline, or Sprungschicht, 'the layer of varying thickness, wherein the fall of temperature equals or exceeds 1·0° C. per metre'.

to warm a column of unit base and height equal to the '*reduced depth*' of the layer from the selected minimum to the summer temperature of the layer. This 'reduced depth' is obtained by dividing the volume of the layer by the area of the surface of the whole lake (through which, incidentally, all heat exchange with the atmosphere must take place). Since the sum of all the 'reduced depths' is equal to the mean depth of the lake, the sum of these heat budgets for the layers gives the total heat budget for the whole column of water as specified by Birge. The maximum value for the total of these budgets is equivalent to Birge's budget (italics, Table 1). The movement of heat within the lake during the summer is shown by tabulating the daily change in the heat budgets for the layers for a number of successive time intervals (Table 2).

(*f*) *Estimation of stability.* Schmidt (1928, p. 151) calculated the stability of a lake in terms of the work necessary to mix the waters completely so that they became iso-thermal; or, 'to shift the centre of gravity of the whole water mass from its position at the time of observation to that when the water was isothermal'. He showed how closely the stability of the stratification in the Lunzer Untersee was related to the wind in the preceding period, as well as indirectly to changes in radiation, evaporation and rainfall. As there are no available data for calculating the energy supplied to Windermere by the wind during the survey, this calculation seems rather barren, especially as it gives no information in any case about the circulation which actually occurred.

The simpler graphical representation of stability, proposed by Münster-Strøm (1933, pp. 29, 32) for comparative purposes, has here been adopted. The values of σ_4 (the difference in weight in grams between 100 l. of water at 4° C. and at the observed temperature) are plotted as abscissae and the depth in metres as ordinates. If the values are taken as positive, the resultant curves can be easily related to the temperature curves, and show the changes in density due to the temperature more conveniently than would a graph of the actual densities. The stability is proportional to the slope of these curves.

4. RESULTS

Temperature of the north basin

Birge & Juday (1914, p. 547) have given good evidence for the satisfactory extent to which observations made near the centre of oscillation of a lake of regular form may be taken as representative of at least the mean temperature conditions in the whole lake. The temperature measurements, taken near the centre of the north basin of Winder-mere, have been used to construct a diagram (Fig. 2) in which the ordinates represent the depths in the lake in metres and the abscissae the months of the year. Each tem-perature measurement was entered at the appropriate depth and time, and isotherms were then drawn for each degree. The diagram was constructed as if the bottom of the lake had always been found at 60 m. (p. 251); therefore it does not show the slight observed tendency for the lowest bottom temperatures to be found when the sounding was deepest, but the tendency was perhaps scarcely significant without further data. The diagram does, however, show clearly the isothermal cooling during the winter; the isothermal warming in April and May and the development of a summer temperature gradient maintained without any sharp thermocline until September. It also indicates the slow warming of the hypolimnion from 7·8 to 8·1° C. during the summer.

These seasonal temperature changes are also shown in Figs. 3 and 4 where ordinates

again show depths in metres, but the abscissae represent the temperatures directly. The records on the left of Fig. 3 show cooling from 13 November 1931 to 3 March 1932; those in Fig. 4 show the spring warming and summer stratification from 15 March to 26 August 1932. The disappearance of the summer stratification between 7 September and 9 October 1932 is shown on the right of Fig. 3, beside the records for the previous winter.

(a) *Winter and spring conditions.* On 13 November 1931 (Fig. 3), when the first measurements were made, there was hardly a trace left of the previous summer's stratification; but the hypolimnion was warmer than at any other time in the year (p. 257). By
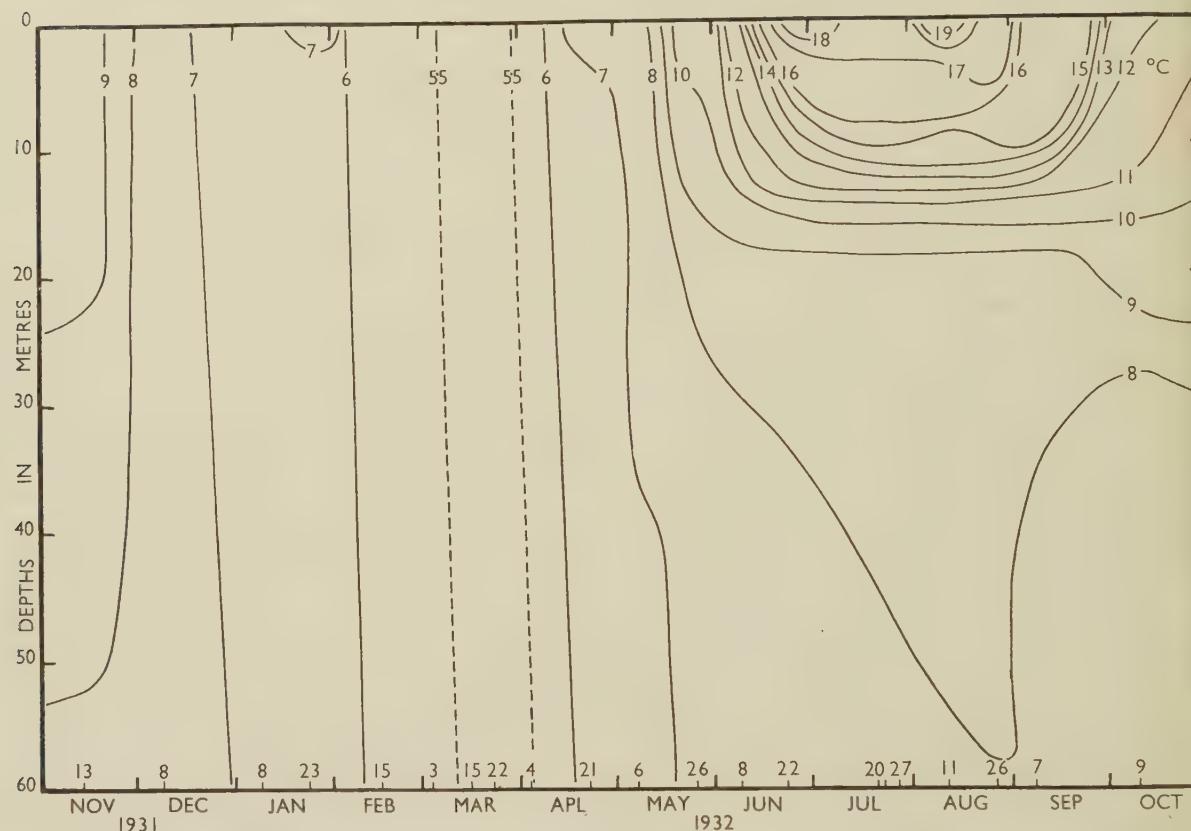
Fig. 2. Temperature at different depths in the north basin of Windermere throughout the year from November 1931 to October 1932 (see text, p. 253). The dates at the foot of the graph show when observations were made.

8 December 1931 mixing was complete and the water was both cooler than before and isothermal throughout. Cooling proceeded until 15 March 1932 (Fig. 4), when the lowest temperatures were recorded. The surface was then 5·2° C., the body of the water was 5·1° and the bottom 4·9°, the very slight stratification possibly being due to the preceding spell of unusually calm frosty weather. Such a stratification would offer no appreciable resistance to renewed wind-mixing, but would at once revert to the isothermal conditions found at all other times during the winter. Isothermal warming, or rather surface warming accompanied by complete mixing, occurred between 15 March and 4 April; but on 21 April there was the first sign of surface warming without mixing.

(*b*) *Summer temperature gradient.* From May to October there was a definite thermal stratification in the water of the lake whenever observations were made. There was always an epilimnion in the wide sense (p. 252) separated by a discontinuity layer from a more or less isothermal and relatively cool hypolimnion. There was considerable oscillation in the surface temperatures, those recorded in May being 12·3° C. on 21st and
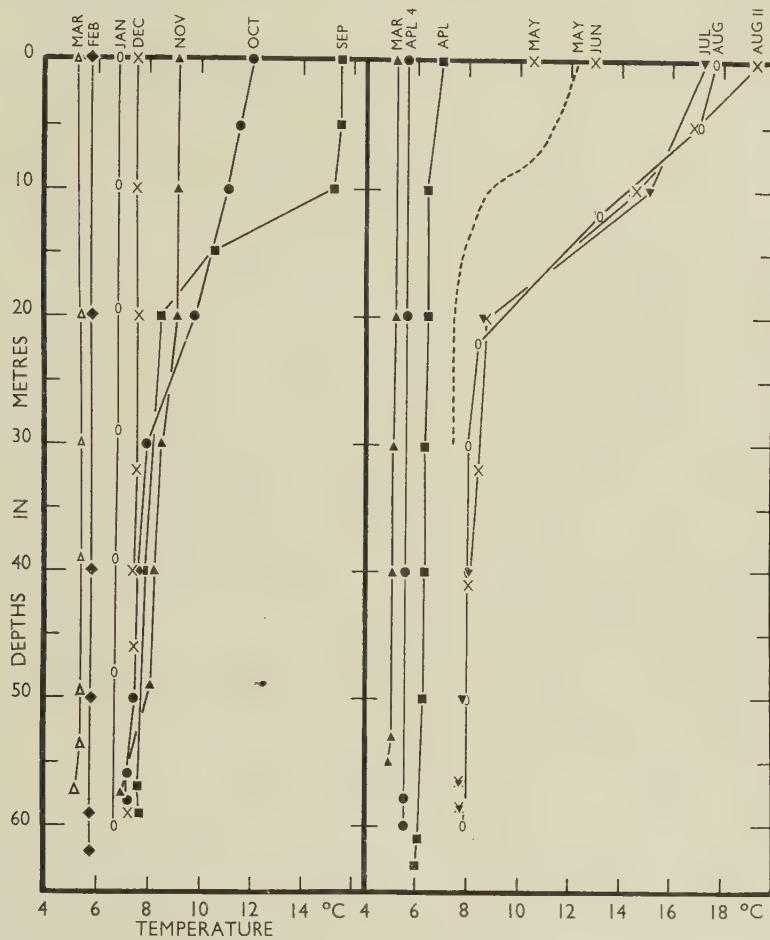
Fig. 3.   Fig. 4.

Fig. 3. Autumn and winter cooling in the north basin of Windermere. Temperature observed at a series of depths on 13 November and 8 December 1931 and 8 January, 15 February, and 3 March 1932, as well as those showing the breakdown in stratification between 7 September and 9 October 1932.

Fig. 4. Spring warming and summer stratification in the north basin of Windermere. Temperatures based, as before, on thermometer readings at a series of depths on 15 March, 4 April, 21 April, 22 July, 11 August and 26 August 1932. The curve for 21 May 1932 is based on readings made with a thermo-electric apparatus (see text below). Surface readings on 26 May and 8 June are marked by ×.

10·6° C. on 26th, and those in June 12·9° C. on 8th and 18·1° C. on 22nd. Between April and July the temperature gradient below the surface is little known (p. 252). Relative observations taken on 21 May (Fig. 4) with the thermo-electric apparatus of Saunders & Ullyott (1937, p. 567) were not accurately calibrated; but water-bottle samples on 8 June still gave cooler readings than in July (7·5° C. at 30 m. and 7·6° C.

at 57·5 m.). The gradient in August, as determined by the water-bottle samples (p. 251), was apparently as variable as it was in 1936 (Ullyott & Holmes, 1936, p. 971). On 11 August 1932 (Fig. 4) the type of gradient recorded was that which is supposed to be the product of calm weather, namely, a high surface temperature and an even gradient to the top of the hypolimnion at 20 m., without any thermocline in the strict sense. On 7 September 1932, when wind-mixing had been aided by surface cooling at nights and consequent convection, the gradient was of the classic type with an isothermal epilimnion down to 10 m. and then a sharp discontinuity layer amounting almost to a thermocline. The actual fall of temperature was 0·9° C. per m. and was the steepest recorded during

Table 1. *Heat storage in the north basin*

Layer m.	Volume m.$^3 \times 10^6$	Reduced depth m.	Winter temp. ° C. 15 Mar.	Heat budgets, 1932, in g.cal./cm.^{2}						
				21 Apr.	21 May	22 July	11 Aug.	26 Aug.	7 Sept.	9 Oct.
0– 2	15·3	1·88	5·2	340	1,330*	2,270	2,640	2,340	1,930	1,280
2–10	49·3	6·04	5·2	910	3,690*	6,650	7,010	7,130	6,190	3,840
10–15	26·1	3·20	5·2	380	990*	3,170	3,010	2,530†	3,200	1,900
15–25	44·3	5·43	5·15	680	1,280*	1,870	1,930	1,770	2,360	2,470
25–35	34·2	4·19	5·1	500	960*	1,340	1,380	1,220	1,280	1,170
35–45	25·3	3·10	5·1	400	710*	920	920	900	850	780
45–55	13·08	1·60	5·1	190	370*	440	450	460	420	380
55–67	4·65	0·57	4·9	70	140*	160	170	170	160	140

				Mean temperatures in ° C.						
Total	212·23	26·01	5·15	6·48	8·79	11·61	11·87	11·50	11·45	9·75
Annual heat budgets in g.cal./cm.^{2}				3,470	9,470	16,810	17,500	16,520	16,400	11,970
Summer heat incomes in g.cal./cm.^{2}				6,460	12,460	19,800	20,490	19,510	19,390	14,960
% heat storage above 15 m.				46·9	63·4	72·0	72·1	72·7	69·0	58·7
% heat storage below 15 m.				53·1	36·6	28·0	27·9	27·3	31·0	41·3

* Thermocouple readings.　　　　　　† Reading taken at 12 m. instead of 10 m.

Table 2. *Changes in heat storage in the north basin in g.cal./cm.^{2}/day.*
Loss of heat shown in italics

Layer m.	21 Apr.– 21 May	21 May– 22 July	22 July– 11 Aug.	11–26 Aug.	26 Aug.– 7 Sept.	7 Sept.– 9 Oct.
0– 2	33·1	15·1	18·8	*– 20·0*	*– 34·4*	*– 20·2*
2–10	92·7	47·7	18·2	8·1	*– 78·1*	*– 73·6*
10–15	20·2	35·1	*– 8·0*	*– 32·0*	56·0	*– 40·5*
15–25	19·9	9·6	2·7	*– 10·8*	49·8	3·4
25–35	15·4	6·1	2·1	*– 11·1*	5·3	*– 3·3*
35–45	10·3	3·3	0·0	*– 1·0*	*– 3·9*	*– 2·4*
45–55	5·9	1·2	0·4	1·0	*– 3·3*	*– 1·3*
55–67	2·4	0·3	0·1	0·4	*– 1·0*	*– 0·5*
Totals	199·9	118·4	34·3	*– 65·45*	*– 9·65*	*– 138·4*

the survey in 1932. In 1936 Ullyott & Holmes (1936, p. 971) recorded a gradient of about 3° C. per m. between 13 and 15 m. on 31 August, after strong wind.

(c) *Autumn cooling.* The heat budgets (Table 1) show that there was a steady, if slight, loss of heat from the lake as a whole from 11 August onward. At the same time the distribution of heat within the lake was being changed, so that by 7 September (Table 2) the lower layers, e.g. 10–35 m., were distinctly warmer than they had been in August, while the surface was being cooled chiefly by wind circulation.

There must also have been some cooling at the surface to account for the appearance of cooler water in successively lower layers of the hypolimnion during most of August

and early September. During the later part of September at least there is evidence that the air temperature was such as to make surface cooling and the setting up of convection currents in the water almost inevitable. The mean daily air temperature for the fortnight before 9 October was only 9·4° C., which was considerably below the temperature of the surface water of the lake, recorded as 11·55° C. on 9 October. The mean of the *minimum* air temperatures during the same period was as low as 4° C., and included three nights on which there was a frost.

While this surface cooling was occurring, Table 2 shows that warm water from the epilimnion was being forced down until the last trace of it reached 25 m. by 9 October, as a result of the wind action involved in this stage of the autumn overturn. A continuation of the same process after 9 October would, presumably, have brought the lake to an isothermal state with a rather lower mean temperature, but with a higher hypolimnion temperature than before, as in November of the previous year (Fig. 3), when the hypolimnion was warmer than at any other time during the survey. The mean

Table 3. *Surface temperatures in ° C., with those below that of maximum density marked by italics*

Months	...	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
West	1907	—	—	—	—	—	—	—	—	14·4	9·0	7·2	*3·2*
	1908	*1·1*	*0·2*	*0·4*	*1·7*	4·4	8·3	11·6	12·6	—	—	—	—
P. M. J.	1931	—	—	—	—	Open water	—	—	—	—	—	9·1	7·5
	1932	6·9	5·8	5·3	6·35	8·8	15·5	17·45	18·5	15·5	12·05	—	—
Wray Castle Boathouse,* monthly averages													
F. B. A.	1933	5·1	4·9	5·4	7·0	10·9	16·9	19·2	18·1	16·3	12·5	7·9	5·4
	1934	5·3	5·2	4·95	5·9	8·8	15·3	19·3	16·2	14·7	11·2	8·0	7·9
	1935	6·5	5·9	6·0	6·8	10·8	14·6	18·3	17·9	14·3	10·5	8·4	6·2
	1936	5·0	2·5	4·4	6·1	11·2	14·8	17·3	16·4	15·5	11·2	8·3	6·6
	1937	6·4	5·6	4·3	6·9	11·3	15·8	16·3	18·7	15·1	12·4	9·1	5·6
	1938	5·4	5·0	6·5	7·9	10·6	13·7	15·6	17·3	14·6	11·3	9·8	7·5
Mean for 6 yr.		5·61	4·85	5·27	6·76	10·60	15·20	17·67	17·43	15·08	11·51	8·60	6·53
Max.		8·0	6·8	7·0	9·9	16·5	20·4	23·1	20·9	18·5	14·8	10·8	8·9
Min.		*3·0*	*0·0*	*1·8*	*4·2*	7·0	10·5	14·2	14·2	12·0	9·0	6·5	*3·0*

* Readings, taken daily about 9.0 a.m., kindly supplied by Freshwater Biological Association.

temperature was 9⋅75° C. in October and 8·79° C. in November. It seems unnecessary, therefore, to postulate from the warmth of the hypolimnion in November 1931, that the hypolimnion had been warmer throughout the previous summer than it was in 1932. Nevertheless, the summer temperature of the hypolimnion may differ considerably from one year to another: for instance, it was over 8·0° C. in August 1932 and only 7·0° C. in August 1936 (Ullyott & Holmes, 1936, p. 971).

(d) *Surface temperatures in other years.* Table 3 gives a series of surface temperatures recorded by West (1909, p. 262) in an exceptionally cold year, and also monthly averages of the daily readings taken in the boathouse at Wray Castle, together with the maximum and minimum values of these readings in each month.* The surface temperatures recorded in open water during the survey are also given (the mean is given if more than one reading was taken); they agree fairly closely with the averages for the same month in the subsequent years, though in the winter they are rather warmer than the average and in the summer they are not so warm as the maxima reached in some other years.

* I am much indebted to the Freshwater Biological Association for permission to publish these results.

Complete freezing of the lake has been recorded occasionally in the past; but in this century the waters have usually remained open all winter. Partial freezing occurred for short periods in the winters of 1908, 1917, 1922, 1929, 1936 and 1940. It can be seen from Table 3 that February 1936 was the only month from 1933 to 1938 in which the average surface temperature fell below 4·0° C.

Temperature of the south basin

Fig. 5 shows the temperatures of the south basin as abscissae and the depth in metres as ordinates. In the winter the water was isothermal at 5·4° C. on 20 February, whereas that in the north basin was still 5·8° C. only five days earlier. In the summer, on 31 August 1932, there was an isothermal epilimnion at 17·3° C. and a temperature gradient of about 0·85° per m. between 10 and 20 m., so that the lower limit of the discontinuity
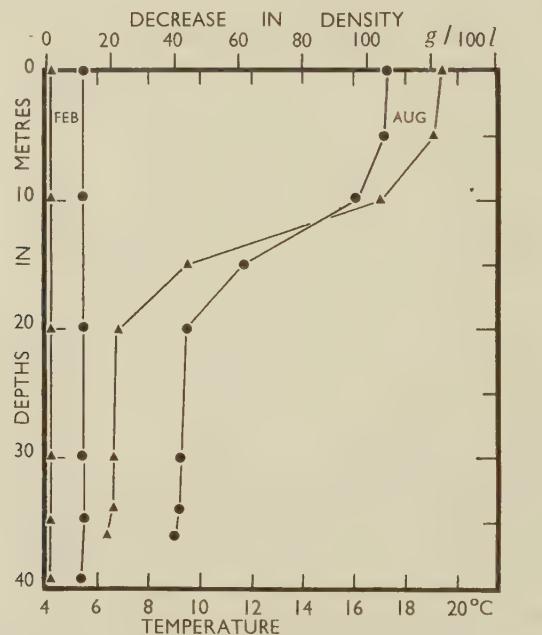
Fig. 5. Winter minimum and summer stratification in the south basin of Windermere. Temperatures (circles) and σ_4 values (triangles, see p. 253) for density differences at a series of depths on 20 February and 31 August 1932.

layer seems to have been rather lower than in the north basin at the same time. The form of the gradient is similar to that found in the north basin on 7 September; but the range of temperature and, therefore, the stability were somewhat higher in the south basin. The hypolimnion in the south basin was warmer than that of the north, being between 9·0 and 9·5 instead of 8·0° C. The differences between the two basins may be attributed to the difference in their depths, the shallowness of the south basin, with a mean depth of only 17·67 m., allowing greater warming of the hypolimnion in the spring before full stratification could be established. The barrier between the two basins by Belle Isle would suffice to maintain this 'depression individuality' (Welch, 1928, p. 431). There are no data for intermediate dates in the south basin such as might show either the time when the stratification became established, or how long it lasted.

Heat budgets

(a) *North basin.* The annual heat budget and the summer heat income (p. 252) for the north basin amounted respectively to 17,500 and 20,490 g.cal./cm.² (Table 1). The percentages of heat stored above and below 15 m., which may be taken roughly as the lower limit of the discontinuity layer, emphasize the relative parts played by epilimnion and hypolimnion in heat storage, and the importance of the former in a relatively shallow lake like Windermere. The shape of the basin is such that when the water is isothermal only 42·7% of the heat is held above 15 m. The successive annual heat budgets for each 10 m. layer (Table 1) show the amounts of heat stored in the different layers of the lake since the winter minimum. Table 2 gives the gain or loss of heat per day for each layer, between successive dates. This shows that there was rapid heating of all layers up to 21 May and then less rapid heating, especially in the hypolimnion, up to 22 July when the maximum heat storage was almost attained. Full circulation was by then clearly over. It may have ceased sooner, but the fact that some heat reached the

Table 4. *Heat storage in south basin*

Layer m.	Volume m.³ × 10⁶	Reduced depth m.	Winter temp. °C. 20 Feb.	Summer temp. °C. 31 Aug.	Heat budget g.cal./cm.² 31 Aug.
0– 2	12·3	1·85	5·4	17·3	2,200
2– 5	15·9	2·39	5·4	17·15	2,810
5–10	22·2	3·33	5·4	16·15	3,580
10–15	17·9	2·69	5·4	11·7	1,690
15–25	27·4	4·11	5·35	9·5	1,710
25–35	17·9	2·69	5·37	9·2	1,030
35–44	4·1	0·61	5·4	9·0	220
Total or mean	117·7	17·67	5·38	12·88	13,230
Summer heat income, g.cal./cm.²			—	—	15,680
% heat storage above 15 m.			58·75	77·65	—
% heat storage below 15 m.			41·25	22·35	—

hypolimnion after 8 June (p. 255) showed that its isolation had periodically been broken down by the wind in this period, for which, unfortunately, there are no other data (p. 252). The further gain in heat between 22 July and 11 August was slight, and the isolation of the hypolimnion was then more nearly complete than at any other time. On 26 August the total heat budget might have been almost the same as on the two previous dates, had it not been for the anomalously low figure given for the 10–15 m. layer (Table 1), based on a reading at 12 instead of the usual 10 m., and therefore near enough to the discontinuity layer to have been too cool to give a fair comparison. If there had been no change in the temperature of this layer between 11 and 26 Auugst, the budget for the later date would have been 17,000 g.cal./cm.², which is closely similar to the two previous budgets.

(b) *South basin.* The annual heat budget and summer heat income for the south basin amounted respectively to 13,230 and 15,680 g.cal./cm.² (Table 4) between 20 February and 31 August 1932, when the only observations were made. These values are lower than those for the north basin, as would be expected from the fact that the mean depth of the south basin is only 17·67 m., as compared with 26·0 m. in the north basin. The heat storage capacity of the former is therefore bound to be less, since both basins are shallower than 30 m. which is considered to be critical for maximum heat storage (p. 265).

5. DISCUSSION

Temperature and biological productivity

The chief interest in the temperature conditions in any lake lies in their effect upon the biological productivity of the water. Other things being equal, the higher the temperature of the water the higher will be the growth rate of the contained organisms. The waters of Windermere were relatively warm in winter, so that growth could continue, albeit slowly, throughout the winter; but in the summer the temperature range was not high and might therefore have been acting as a limiting factor upon the summer growth rate.

More important perhaps is the indirect effect of the temperature upon the circulation of the water and therefore upon the supply of nutrient salts from the hypolimnion to the phytoplankton in the illuminated part of the epilimnion. In Windermere there is as a rule no winter temperature stratification and no stagnation of the hypolimnion. Interest therefore turns upon the summer stratification and how much this impedes the circulation of the lake waters. This may be considered from two aspects: the qualitative aspect of how completely the stratification may isolate the hypolimnion from the epilimnion, and the quantitative aspect of the duration of this isolation.

(a) *The degree of isolation of the hypolimnion*. This depends upon the balance between the theoretical stability of the lake, due to the effect of temperature upon the density, and the actual wind force applied to the lake surface to cause mixing of epilimnion and hypolimnion. It follows that the stability of the thermal stratification at any given time is not alone sufficient to determine the degree of isolation that will follow. In addition to the incidence and strength of the wind, the form and extent of the lake surface and the amounts of rainfall and evaporation will all influence the degree of isolation following upon a given initial temperature gradient. To take an extreme case it is clear that in a prolonged calm there would be no circulation even in a lake with no appreciable temperature gradient at all.

The relative increase in stability with rising temperature is represented graphically in Fig. 5 for the south basin. This graph emphasizes the importance of the actual temperature range, as well as the steepness of the gradient in the discontinuity layer, in controlling the density differences upon which the potential stability of the system depends (Birge, 1910, p. 989). The σ_4 curves are directly comparable with those given by Münster-Strøm (1933, figs. 16–20, pp. 29–32) for some of the Norwegian lakes; and also with those given for the north basin of Windermere and other lakes in Fig. 6 A, B.

Some evidence of the effect of this degree of stability upon the actual circulation that took place in Windermere during the summer of 1932 may be gleaned from the heat budgets, calculated for successive dates during the period of thermal stratification from April to October 1932 (Tables 1 and 2). It may be assumed that transference of heat by conduction from one depth in the lake to another would be so slow that any appreciable *increase* in the heat content of the lower layers must have been due to wind causing a mechanical transference of a body of water from a warmer upper layer to the lower layer in question, and presumably also causing a reciprocal transference of cool hypolimnion water upwards into the epilimnion. Conversely, it may be assumed that any marked *decrease* in the heat content of the lower layers must have been due to the downward distribution of cooler water from the surface by convection, with or without aid from the wind. At the same time, minor variations in temperature in the lower

layers of the lake, and in the derived heat budgets, may be insignificant. They may be due to currents or to a temperature seiche or some other chance fluctuation or movement within the hypolimnion. Hutchinson (1938, p. 67) has given further evidence in support of Alsterberg's theory of the occurrence of microstratification in the hypolimnion of many lakes during their stagnation: this is accompanied at least by horizontal streaming, if not also by slight vertical movements. Wedderburn (1912, passim) showed that the physical seiche of the lake surface might be accompanied by rocking of the lower isotherms producing what he called a temperature seiche. Observations in Windermere may easily have been affected by either of these factors or by currents of water flowing in from the Brathay and not reaching equilibrium with the main body of the standing water before passing the sampling station. Mortimer (personal communication) has found in other years that the inflow is on the average about 1° C. cooler than the surface water of the lake. The volume of this inflow between May and September may be over 20 % of the whole lake contents, and must cause appreciable disturbance within the lake until it reaches its proper level.

Table 2 shows that the isolation of the hypolimnion was never absolute for any length of time; but between May and October the rate of change of the heat storage below 15 m. is much smaller than in the fully mixed layers above. The daily changes are especially small between 22 July and 7 September, and insignificant between 22 July and 11 August, when there seems to have been a very considerable degree of isolation of the hypolimnion. The lowest exchange rate between hypolimnion and epilimnion during the summer was between July and 11 August, when the hypolimnion as a whole was losing 5·5 g.cal./cm.^{2} in 24 hr. This was little compared with a change of 80 g.cal./cm.^{2} in 12 hr. recorded by Münster-Strøm (1932b, p. 267) in the hypolimnion of the sheltered Lilla Le. The relatively small heat exchange below 15 m. between July and October can also be seen by contrasting the total changes during that period both with those before July and those above 15 m.:—

	May–July	22 July–11 Aug.	11–26 Aug.	26 Aug.–Sept.	7 Sept.–Oct.
above 15 m.	6,080	580	− 660	− 680	− 4,300
below 15 m.	1,270	110	− 320	+ 560	− 130

Between August and September there was considerable downward circulation of heat, with little loss to the air. Much more frequent and closely spaced observations of temperature in the hypolimnion might elucidate the question of heat transference through different types of discontinuity layers under varying conditions and help to distinguish temperature changes due to mixing with the epilimnion from those caused by temperature seiches and other minor factors.

(b) *Duration of isolation of the hypolimnion.* This factor in production biology seems to be of great importance, especially in relation to the seasonal changes in the length and intensity of daylight available for photosynthesis. But it seems to have received relatively little attention, perhaps because much of the work upon stagnation in individual lakes has only been based on two sets of observation in the year: one at the time of the winter minimum and the other at about the time of the summer maximum. In Windermere, although *some* thermal stratification was apparent for seven months from April to October, the heat budgets (Table 2) show that *isolation was brief, only being certainly effective for about one month*, from mid-July to mid-August.

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*Comparisons between Windermere and other lakes of 'Coastal'
and 'Continental' type*

(*a*) *Stratification and hypolimnion temperature.* The type of stratification established in any lake is dependent upon two main sets of factors: (i) the *climatic* factors, which control the relation between windy and warming periods, and are themselves mainly dependent upon the geographical situation of the lake, but are subject to some variation in weather from year to year; and (ii) the *morphometric* factors, of size, shape and depth, controlling the influence of the climate upon the amount of heat absorbed and the circulation produced by the wind. The *morphometric* factors are fixed for any given lake, but should be taken into consideration in making comparisons with other lakes. The differences already noticed (p. 258) between the north (Fig. 6B, ■ '32), and south (▲ '32) basins of Windermere afford an example of the effect of depth: within limits, the shallower the lake the more marked is its stratification likely to be and the earlier will it be established.

Among *climatic* factors, the effect of wind in one year may be to break up the early stages of stratification and produce a warm hypolimnion, while in another year stratification may become more stable before the wind comes and the hypolimnion may then remain isolated and cool. As Wedderburn put it (1910, p. 132) 'the stronger the wind in the summer, the higher will be the bottom temperature'.* Such effects may be seen in the σ_4 curves, in Fig. 6B, for some relatively shallow lakes comparable with Windermere. In the abnormally hot summer of 1911, Loch Earn (*e* '11 from Wedderburn, 1912, p. 672) and, to an even more marked degree, the Lunzer Untersee (L '11 from Ruttner, 1929, p. 19) acquired a well-marked discontinuity layer overlying a cool hypolimnion. This may be called a 'continental' type of stratification. In the more normal summer of 1912 the curve for the Lunzer Untersee (L '12 from Ruttner, 1929, p. 19) contrasted sharply with that for the same month in the previous year, by having a warmer hypolimnion isolated by a much less steep temperature gradient, of the 'coastal' type. Unfortunately, Loch Earn has not been examined in any other year, but it is difficult to believe that it would not often be found to have a 'coastal' curve similar to those for the other Scottish lochs, such as Loch Garry (*o* '09, from Wedderburn, 1909, pp. 134-5). The similarity between the latter and the curve for Windermere (■ '32) is rather remarkable, but that for Loch Garry was recorded in late July and that for Windermere in September. There was a considerable contrast between this curve for Windermere itself in 1932 and that in August 1936 (*x* '36, from Ullyott & Holmes, 1936, p. 971). The surface temperatures (Table 3) show that the water was unusually hot in May 1936, so that an early stratification over a cool hypolimnion may have become established at that time. On the whole it does not seem as though the weather in the English Lake District was particularly abnormal during the survey in 1931-2, except perhaps for a rather long drought in February and March; but, as this would not affect the summer stratification, the results may be compared with conditions found in other lakes to obtain some idea of the *geographical* factors involved. The closest similarity might be expected between Windermere and lakes in the coastal regions of Scotland and Norway. ·

* Wedderburn's converse statement that 'the stronger the wind in the winter the lower will be the bottom temperature' is *only* applicable to lakes like Loch Ness (where he was working) that are so deep or sheltered that they do not readily or necessarily reach an isothermal condition in winter.
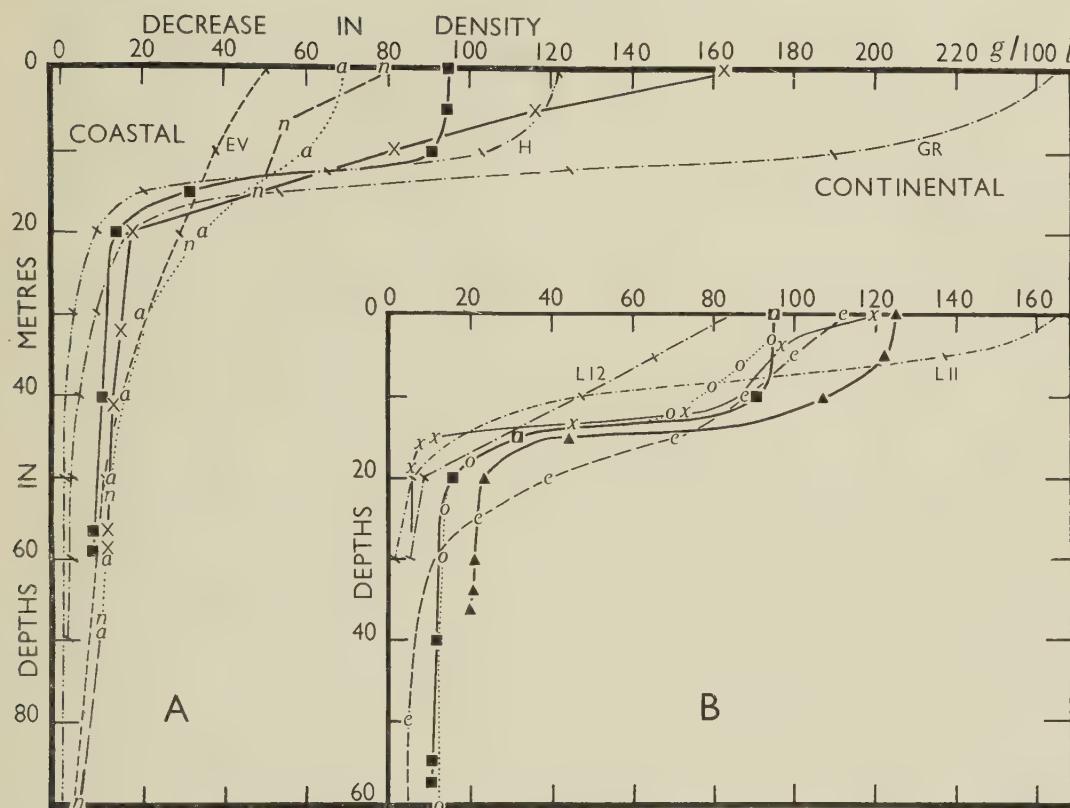
Fig. 6. Density differences at a series of depths, shown as σ_4 values, for comparison of the stability of various lakes at the height of the summer thermal stratification. A, Typical 'Coastal' and 'Continental' Lakes, compared with Windermere, to show the effect of geographical position upon stability curves. B, Shallower lakes, in different years to show the effect of weather (e.g. the very hot summer of 1911) upon stability curves. Observations marked by symbols on curves for lakes within the British Isles (those for Windermere as in Figs. 3–5):

$a...a$	Loch Awe, western Scotland, 20 Aug. 1930
$e...e$	Loch Earn, central Scotland, 11 Aug. 1911
$n...n$	Loch Ness, north-western Scotland, 10 Aug. 1907
$o...o$	Loch Garry, western Scotland, 25 July 1909
$X—X$	Windermere, north-western England, 11 Aug. 1932
$x—x$	Windermere, north-western England, 31 Aug. 1936
■ –■	Windermere (north basin), north-western England, 7 Sept. 1932
▲—▲	Windermere (south basin), north-western England, 31 Aug. 1932

Observations marked by oblique strokes on curves for lakes in other countries:

EV	Evangervatn, western Norway, 15 Aug. 1928
GR	Green Lake, central U.S.A., 20 Aug. 1905
H	Holsfjord, eastern Norway, 17 Aug. 1930
L 11	Lunzer Untersee, Austria, Aug. 1911
L 12	Lunzer Untersee, Austria, Aug. 1912

Holsfjord, Evangervatn, and Loch Ness are all too deep for their bottom values to be shown on the graph, but in each case they fall in line with those hypolimnion values that are shown.

17-2

Münster-Strøm (1931 a, p. 355) has defined two types of lake in Norway, based upon climatic factors: the Atlantic and the Continental. His *Atlantic*, or 'coastal' type of lake, lies near the west coast of Norway and includes Evangervatn (Fig. 6 A, EV '28, from Münster-Strøm, 1930, p. 108), 'where the warming begins early and increases gradually, while winds are generally strong, the *heat is carried far down into the lake and the "Sprungschicht" is deep and not well-marked*. The deep water takes up much heat (5·1° C. at 100 m.) while by continually mixing with these lower layers the surface waters remain comparatively cool (12·2° C.)'. His '*Continental*' type of lake lies inland in eastern Norway and includes deep lakes like Holsfjord (Fig. 6 A, H '30, from Münster-Strøm, 1932 a, p. 17), where 'warming of the upper layers in early summer increases rapidly so that the *density differences between the surface and deep water quickly become so great that even strong winds cannot produce any deep-reaching mixing. The "Sprungschicht" becomes well-marked* and lies in late summer at a depth of 12–15 m. The temperature of the surface is high (17·13° C.), and that of the deep water scarcely different from the winter minimum'* (4·18° C. at 100 m., 3·72° C. at 250 m.).

The σ_4 curves in Fig. 6 A are given as a basis for comparison between the lakes of these two Norwegian types, Windermere and some lakes in Scotland, central Europe and the United States of America. Green Lake (Fig. 6 A, GR '05, from Birge & Juday, 1911, p. 148) lies in the continental region of America and affords an exaggerated version of Münster-Strøm's 'continental' type, with its high surface temperature of 23° C., its sharp thermocline and immense stability. It is both shallower (maximum depth 70 m.) and farther from any coast than Holsfjord (H '30). The deeper Scottish lochs belong as clearly to the 'coastal' type. Loch Ness (n '07, from Wedderburn, 1907 b, p. 471) only differs from Evangervatn (EV '28) in having a slightly warmer epilimnion causing a more marked discontinuity layer above 20 m. The hypolimnion temperature of 5·78° C. at 210 m. was also slightly warmer than the supposedly warm hypolimnion of Evangervatn. In 1930 Loch Awe (a '30, from the writer's unpublished observations) was also closely similar to Loch Ness, although its maximum depth is only 92 m.: in 1927 the hypolimnion had been found to be rather warmer, with an even less well-marked discontinuity layer (Jenkin, 1930, pp. 29–30). The differences between the curve for Loch Awe and that for Holsfjord may be attributed with some certainty to the differences in their geographical position, since both are based on observations made in August 1930. The effect of their respective depths would be to minimize this difference.

The warm hypolimnion of the north basin of Windermere in August (X '32) and September 1932 (■ '32) was similar to that of the other 'coastal' lakes; but the influence of its relative shallowness is apparent in its warmer epilimnion and more marked discontinuity layer, as compared even with Loch Awe. This effect is even more marked in the south basin (▲'32). The actual epilimnion temperatures in Windermere were similar to those in Holsfjord, but they would not result in so great stability owing to the warmer hypolimnion. There is no evidence as to whether the coastal position of Windermere exposes it to stronger winds than Holsfjord, as well as to less rapid warming in the spring.

If sufficient allowance is made for variations in weather and differing morphometric factors, it seems clear that this grouping of lakes into coastal and continental types could usefully be extended to other lakes in the northern temperate regions of Europe and America and even to Japan.

* The italics, as well as the translation, are mine. P. M. J.

(*b*) *Duration of isolation of the hypolimnion.* The curves in Fig. 6 A, B are all based upon results obtained at the height of the summer stratification and give no indication of the length of time for which the stratification persists. As has been pointed out already (p. 261), this time factor is of great importance in the productivity of the lake, and it is one which differs greatly in different lakes. Whereas in Windermere the stratification only isolated the hypolimnion from the circulation effectively for about *one* month, the stratification in a continental lake, such as Green Lake, is established early and produces not only very complete isolation of the hypolimnion but an isolation that may last for upwards of *three* months. The duration of the isolation may well afford as great a distinction between the shallower coastal and continental lakes, as does the form of their temperature gradients; though in effect the brevity, or absence, of isolation in the coastal lake may be off-set by the limitation of their productivity caused by their lower range of temperatures.

(*c*) *Heat budgets.* Birge & Juday (1914, p. 546) showed that, apart from small oscillations, similar to those in July and August in Table 1, the amount of heat stored in any lake usually remains substantially the same during most of the summer stagnation. Although Birge (1915, p. 195) has found variations of as much as 100% in the heat budgets for the same lake in successive years, Münster-Strøm (1933, p. 38) claims to have confirmed Birge's view that, on the whole, lakes in similar latitudes, with a mean depth of at least 30 m., usually have similar summer heat incomes; this income, if not limited by extraneous factors, he calls the climatically possible maximum for the latitude in which the lake lies. Further heat, reaching the surface of the lake after this maximum is attained, instead of being stored, is lost* by reflection, radiation and not least by evaporation (Harvey, 1925, p. 691). In a hot summer the increased loss due to evaporation alone may more than offset the extra heat supplied to the lake, as compared with a cooler season. Similarly, as Münster-Strøm (1931*a*, p. 355) has shown, the widely differing temperature gradients of Evangervatn and Holsfjord† (Fig. 6 A), due to their respective coastal and continental positions, do not cause any appreciable difference between their summer heat incomes (Table 5).

It is difficult to make direct comparison between the heat storage in Windermere and in other lakes, because for one thing the mean depth of even the north basin is not as great as Birge's critical 30 m., and for another, the mean winter temperature is rarely so low as 4° C. from which the summer heat income is calculated. An arbitrary allowance may be made for the increase in summer heat income that might follow if the mean depth of the north basin were 30 m. instead of 26 m. while still having the same hypolimnion temperature; but the resulting increase from 20,490 to 22,010 g.cal./cm.² does not make much difference. Again it may be assumed that if the winter temperature had been so low as 4° C. the summer warming would only have been rather slower and later in attaining an amount of heat storage closely similar to that actually found.

The summer heat incomes for Windermere are compared in Table 5 with those recorded by Münster-Strøm for a selection of Norwegian lakes from altitudes that do not differ too widely from that of Windermere. Higher altitudes definitely reduce the summer

* Wedderburn (1910, p. 101) showed that loss of the heat, supplied to the water surface by radiation, amounted to 75% in Loch Ness and 88% in Loch Garry.

† Holsfjord achieved its high heat income in spite of its ice-cover remaining until 20 April (Münster-Strøm, 1932*a*, p. 24), a date by which Windermere had already been warmed to over 6° C.

heat income: for instance Lilla Le lies in nearly the same latitude as N. Vangsvatn (Table 5) and has the not dissimilar depth of 20 m.; but its altitude is 135·5 m. and its summer heat income is only 9090 g.cal./cm.^{2} (Münster-Strøm, 1932b, p. 267). The lakes in Table 5 are arranged by latitude and then separated into those with mean depths below and above the critical 30 m. Incidentally it appears as if even a depth of 37 m. may not have been sufficient to ensure the maximum heat storage in Ø. Vangsvatn.

In both the shallow and the deep series of lakes there is a decrease in heat storage in higher latitudes. From this point of view the heat storage in Windermere falls into line quite satisfactorily among the shallower lakes; but the arbitrary value put forward for its income if it had been 30 m. deep is obviously too low for the deep series if this is to increase proportionately with decreasing latitude. It is unfortunate that Wedderburn gave no comparable heat incomes for the Scottish lochs. It is to be hoped that a budget will soon be obtained for Wastwater, which should be deep enough to give a true estimate

Table 5. *Summer heat incomes for Windermere and some Norwegian lakes*

Lat. °N.	Lake	Altitude m.	Mean depth m.	Summer heat income g.cal./cm.^{2} Under 30 m.	Over 30 m.
54° 20′	Windermere: South	39·3	17·6	15,680	—
	North	39·3	26·0	20,490	—
	Arbitrary	*39·3*	*30·0*	—	*22,010*
60°	Holsfjord (1932a, p. 17)	64	114·0	—	22,058
60° 50′	Evangervatn (1930, p. 108)	10	46·0	—	23,642
	N. Vangsvatn (1931b, p. 529)	50	23·0	14,866	—
	Ø. Vangsvatn (1931b, p. 528)	50	37·0	—	19,555
*61° 37′	Breimsvatn (1933, p. 35)	61	130·4	—	18,597
61° 59′	Strynsvatn (1933, p. 36)	26·8	130·0	—	19,823
	Hornindalsvatn (1933, p. 35)	53	237·0	—	19,484
68°	Festhelsvatn (1938, p. 5)	8	20·3	7,452	—
	Åvatn (1938, p. 5)	5	27·2	12,341	—
	Solbjørnvatn (1938, p. 5)	70	75·0	—	7,972
	Studalsvatn (1938, p. 5)	77	73·6	—	9,638

All values, except those for Windermere, are taken from Münster-Strøm, 1930–8.

* Not 51° as given by a slip in Münster-Strøm (1933, p. 7).

of the maximum amount of heat storage that is possible in the climate and latitude of the English Lake District.

Taking annual heat budgets instead of summer heat incomes, Birge (1915, p. 195) found high values between 25,000 and 40,000 g.cal./cm.^{2} for many European and American lakes at similar or lower latitudes than Windermere, for which this budget was only 17,500 in 1932. The lakes quoted by Birge were all deep, as compared with Windermere; but they included one curious exception in the budget for Como in 1888–9 which amounted only to 17,000 g.cal./cm.^{2}

(*d*) *Autumn breakdown of stratification.* During the autumn Windermere lost heat from the lake as a whole (Table 1), although there was a gain in heat in some layers of the hypolimnion. The cooling of the surface, due to loss of heat to the air, apparently set up convection currents and so played a considerable part in aiding the wind circulation. In contrast to this, Wedderburn claimed (1907a, p. 14) that in Loch Ness 'while the surface temperature *decreases* (in autumn) the total quantity of heat in the loch may *increase* for a time'. This could presumably only have occurred if the stratification, which is never very stable in Loch Ness, were entirely broken down by wind action, and the

surface cooling were only due to mixing with cooler waters from below. The air must still have been supplying some heat to the surface waters in order to increase the total heat content of the lake. Such conditions would seem to be impossible in the stable continental lakes and improbable even in the shallower and more stable of the coastal lakes, such as Windermere.

6. CONCLUSIONS

The results of the survey of the seasonal temperature changes in the waters of Windermere show that the lake conforms to Whipple's (1927, p. 154) second order of Forel's unfortunately named 'tropical' type of lake, in which the surface temperature is never below 4° C., and the bottom temperatures undergo annual fluctuations but are never far from 4° C., so that there is a continuous period of circulation in the winter. In Windermere the surface temperature may fall below 4° C. and even reach freezing-point in some winters; but this rarely lasts for a sufficient length of time to warrant the lake being classified as 'temperate', even in the coldest years. The summer stratification is such that a discontinuity layer is present for some months; but a true thermocline only develops occasionally. Nevertheless, the successive heat budgets during the summer of 1932 (Tables 1 and 2) show clearly that there was a considerable degree of isolation of the hypolimnion from the general circulation of the lake for at least one month, from mid-July to mid-August. Prior to this the hypolimnion became warmed by mixing with the epilimnion and its temperature was raised from the winter level of 5° C. to a maximum of just over 8° C. The temperature characteristics of the summer stratification have much in common with the shallower lakes of Münster-Strøm's 'Atlantic' or coastal type, among which many of the Scottish lochs should also be included. The conditions in these lakes may be contrasted with those in the 'continental' lakes of eastern Norway, mid-Europe and the United States of America. The two basins of Windermere show a certain degree of 'depression individuality' attributable to the greater shallowness of the south basin as compared with the north.

7. SUMMARY

1. The temperature of Windermere was surveyed from the Freshwater Biological Association's laboratory at Wray Castle between November 1931 and October 1932.

2. The geology, rainfall and outflow of the lake are outlined, and a bathymetric map (Fig. 1) is given, based on the echo-sounding survey of 1937. The lake is divided into north and south basins with mean depths of 26 and 17·7 m. respectively.

3. The routine included the measurement of temperatures in water bottle samples from a series of seven or eight depths in both basins.*

4. 'Epilimnion' in a wide sense and 'discontinuity layer' in Wedderburn's sense are used in describing the summer thermal stratification, from which a true thermocline may be lacking.

5. Seasonal temperature changes in both basins are presented in Figs. 2–5 and differ because the south basin is the shallower. Both conform to Whipple's second order of 'tropical' lakes, though freezing occurs in some years for short periods.

6. The steepest summer temperature gradient recorded in the lake in 1932 was 0·9° C. per m. Successive heat budgets for each 10 m. layer showed that this gradient was

* Full data are being deposited with the Freshwater Biological Association and the British Museum (Natural History) London.

sufficient to maintain almost complete isolation of the hypolimnion from 22 July to 11 August and partial, but probably significant, isolation for some longer time. The values of σ_4 (p. 253) in Figs. 5 and 6 present graphically the stability of this and other lakes.

7. The autumn turnover was facilitated by surface cooling and convection currents, unlike that in Loch Ness.

8. The annual heat budget and summer heat income for the north basin were 17,500 and 20,490 and for the south basin 13,230 and 15,680 g.cal./cm.^{2} respectively; neither basin has as great a mean depth as 30 m. which is considered critical for maximum heat storage in any given latitude.

9. The relation of biological productivity to the temperature range and to both the duration and the degree of summer isolation of the hypolimnion is stressed.

10. The summer stratification and hypolimnion temperature, the degree and duration of hypolimnion isolation, the heat storage and the break-down of the stratification in autumn in Windermere are compared with those in lakes in Central Europe, Scandinavia, Scotland and North America. The Scottish lochs and the English lakes conform to Münster-Strøm's 'Atlantic' or 'coastal' type, of which Windermere is a shallow variety. They are contrasted with the 'Continental' type in Fig. 6.

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CANADIAN ARCTIC WILD LIFE ENQUIRY, 1940–41*

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(*With Plates 6 and 7 and 4 Figures in the Text*)

1. GENERAL RESULTS

POPULATION trends in the arctic fox (*Alopex lagopus*) during 1935–41 are roughly shown from the percentage of observers who reported *increase* in their replies to the annual wild life questionnaire:

	1935–6	1936–7	1937–8	1938–9	1939–40	1940–1
Eastern Arctic	1	57	82	16	13	57
Western Arctic	8	11	50	64	9	88

In the Eastern Arctic white fox reached a general peak in 1937–8 and then declined sharply. In the Western Arctic there was no general peak in any of the years 1935–40, though 1938–9 was a good year in the interior barren lands and on Victoria Island. However, in 1940–1, for the first time in six years, there seems to have been a simultaneous upswing in fox populations throughout almost the whole of the Arctic and Subarctic: the main exceptions are Northern Labrador (group 1), James and south Hudson Bays (group 3). Most of the latter area is outside the animal's breeding range, and if observations from here and group 1 (see below) are omitted, *increase* for the East becomes 85 instead of 57%.

In the Eastern Arctic, recovery in foxes was to be expected from the information that lemmings (*Lemmus, Dicrostonyx*) were improving in the year before (61% of reports were *increase*). In the Western Arctic, however, only 14% of observers considered that lemmings were increasing in 1939–40, and their reports thus gave no advance information about the fox recovery. During 1940–1 lemmings continued to increase in the Eastern Arctic and started to do so at many places in the West.

The map of increase in snowy owls (*Nyctea nyctea*) corresponds in general with the pattern of increase in lemmings, and mice in group 3. As with lemmings, recovery in these owls was beginning in the east in 1939–40 but was not apparent in the West.

The year 1940–1 was therefore one of general improvement in arctic foxes, lemmings and snowy owls from Hudson Strait to Coppermine or the MacKenzie River delta.

Sledge dogs suffered from epidemics of 'distemper' on the west coast of Hudson Bay, at Coppermine and on Victoria Island.

2. REGIONAL VARIATIONS IN THE CYCLE: GROUPS 1–8

Northern Labrador coast (group 1). Along this coast the last peak in all three animals was about a year later in passing than it was elsewhere in the eastern Arctic, and 1939–40 became the bottom year of the cycle. In 1940–1 a little recovery in lemmings and 'mice' was apparent at three places, and at two others an increase in snowy owls was noticed.

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* Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

Improvement in arctic foxes may be expected during 1941–2, partly by breeding and partly by migration on the sea ice from farther north.

Northern Quebec and Baffin Island (groups 2, 6 and 7). All three animals reached the bottom of the cycle in 1938–9. In the two following years snowy owls and lemmings (*Dicrostonyx* spp. and, except in Quebec, *Lemmus trimucronatus*) showed a substantial recovery: without exception reports agreed that lemmings had increased or remained abundant in 1940–1. Foxes, which were still decreasing at most places the year before showed a general improvement in 1940–1, though without reaching great density. The interior west of Ungava Bay was exceptional in having had two years of recovery in foxes. At Clyde River on Baffin Island this was also the second year of increase.

Payne Bay. 'White fox were much more abundant than they have been for some time, but they were not as plentiful as they are some years. In fact there were no foxes on the coast at all.' (L. Coates.)

Cape Smith. 'White foxes were abundant inland throughout the season, but very few along the coast. Owls and lemming were plentiful everywhere. Fox burrows are reported full of cubs this spring.' (P. A. C. Nichols.)

Povungnetuk. 'Snowy owls migrated early last fall, and only a few were reported seen during the winter. Lemmings and foxes are on the up-grade and should reach the peak of their cycle 1941–2.' (R. Cruickshank.)

Lake Harbour. 'Lemming and snowy owls were very plentiful during the outfit. In fact the most plentiful we have known them to be since 1930. White foxes were quite plentiful inland, but practically none on the coast, and had better hunting conditions prevailed, returns would have been appreciably higher.' (J. Bell.)

Cape Dorset. 'Foxes, in majority, were fatter winter 1939–40; despite the fact that lemmings have been much more abundant winter 1940–1. However, foxes during winter 1940–1 were not hungry.' (O. M. Demment.)

36. *Pangnirtung.* 'Foxes were more abundant than the game returns indicate, but were not hungry and therefore hard to trap.' (D. P. McLaughlan.)

Clyde River. 'Signs of foxes very good all over about mid-October, but when trapping started they were not hungry, hares being very numerous and much hunted by foxes. Foxes moved northwards end of November and early December...southward in April and at present are very numerous all along coast, but scarcer near head of fiords. Lemmings are much more abundant this month [May] than last month.' (J. G. Cormack.)

Arctic Bay. 'Although fox returns were much less...the actual abundance of white fox was much greater. In October and November there were great numbers passing south. Signs were less during January and February, but from March onwards have been fairly numerous.' (T. Ross.)

Eskimo Point and Tavane. Lemmings have continued a slow three-year recovery from the low point in their cycle in 1937–8. In that year some increase was still reported in arctic foxes, but with this exception little increase either in foxes or owls was reported for the three years previous to 1940–1.

Eskimo Point. 'Lemming and mice more abundant both locally and inland than for some years. In May 1941 many mice were found dead in their nests after spring thaw. Judging from the amount of nests noted mice must have been very abundant during winter but owing to heavy snowfall this was not apparent until spring. An estimate of one dead mouse to every seven nests examined could be given. This is my own personal observation in recent weeks.' (W. C. Brownie.)

Southampton Island, Repulse Bay and Chesterfield Inlet (groups 4 and 5). At these posts lemmings started the upward swing of their cycle well ahead of any other parts of the Arctic and 1940–1 was the fifth year since their previous peak. Reports about lemmings and snowy owls at Chesterfield are unfortunately conflicting but give no grounds for
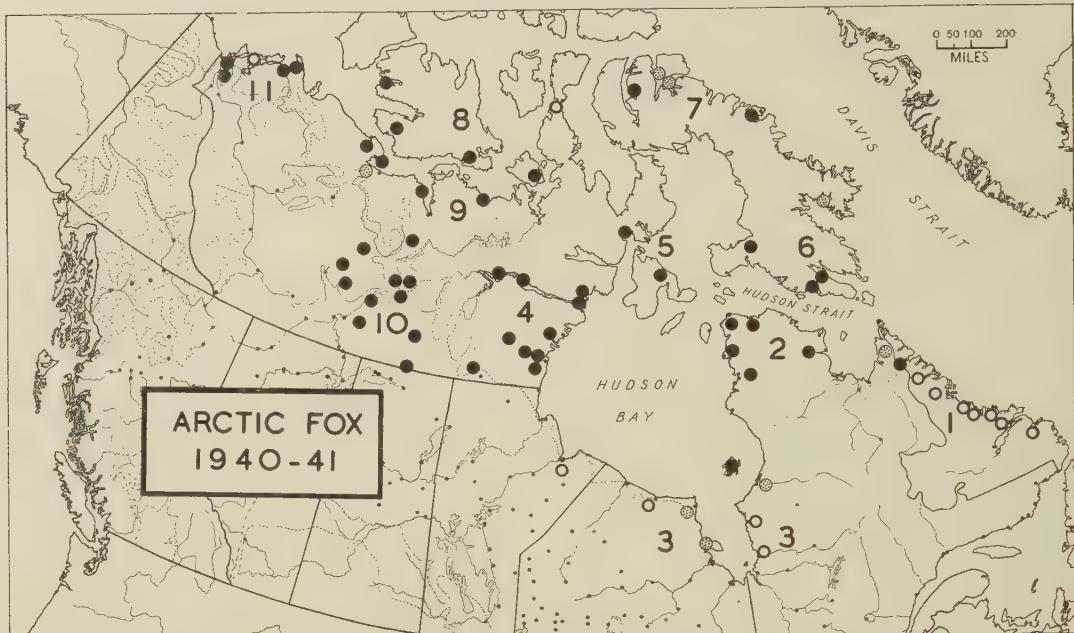
Fig. 1. Reports about the arctic fox population in 1940–1 compared with 1939–40. Each symbol is at the approximate centre of an observer's area: solid black discs are INCREASE; plain circles are DECREASE; circles with small dots are NO CHANGE, NOT ABUNDANT. The larger black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.
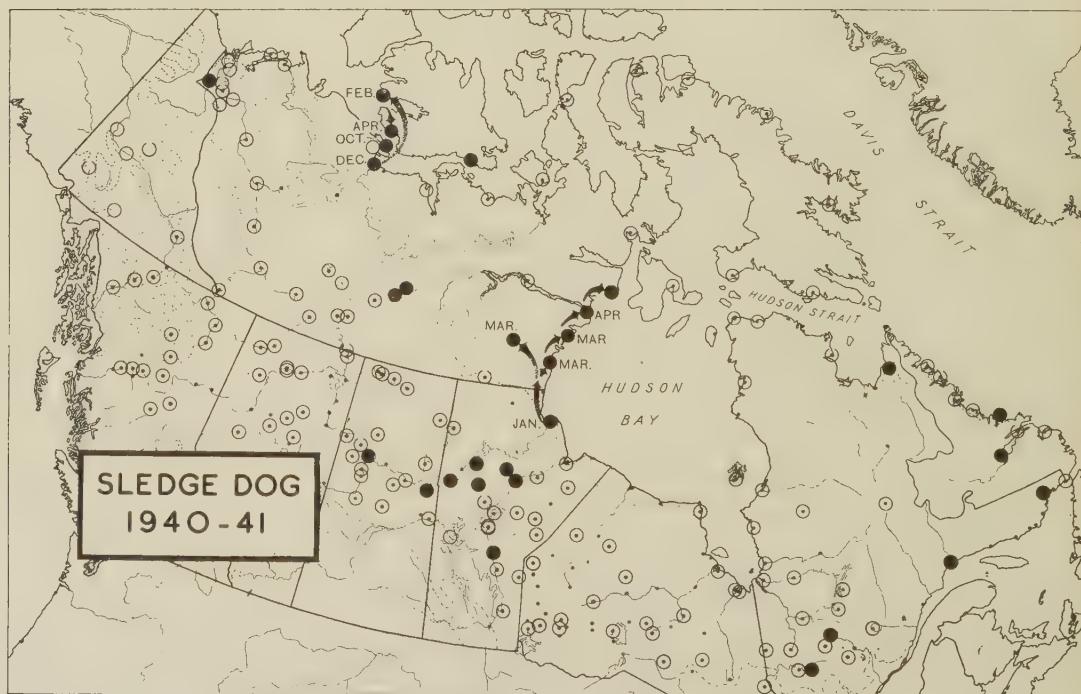
Fig. 2. Prevalence of disease among sledge dogs in 1940–1. Reports of disease, mostly serious, are shown by solid black discs; disease entirely absent by plain circles; other reports by broken circles.
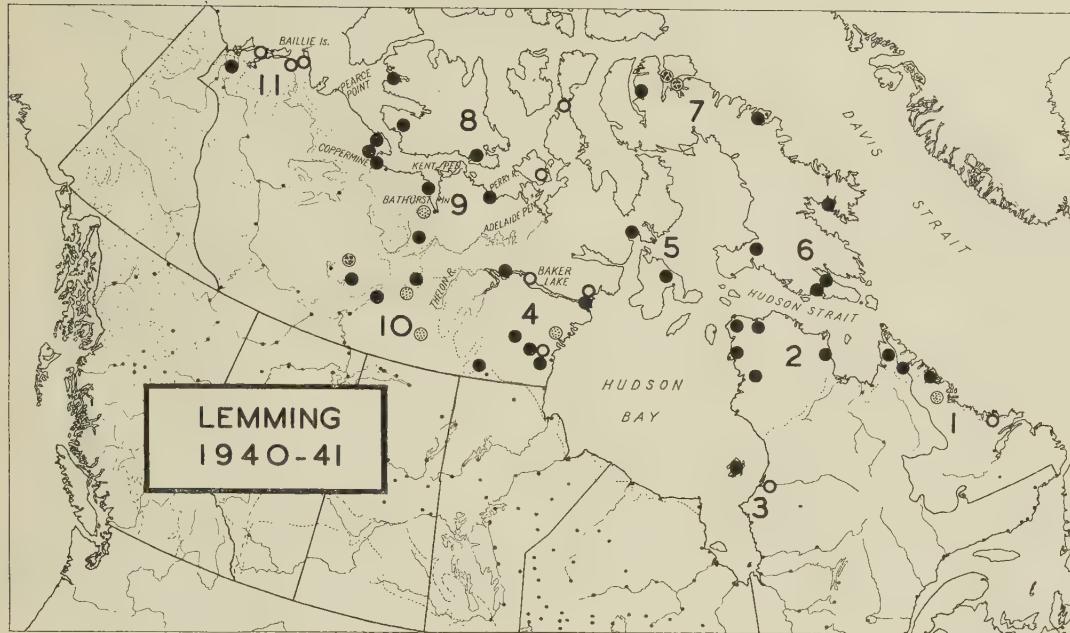
Fig. 3.
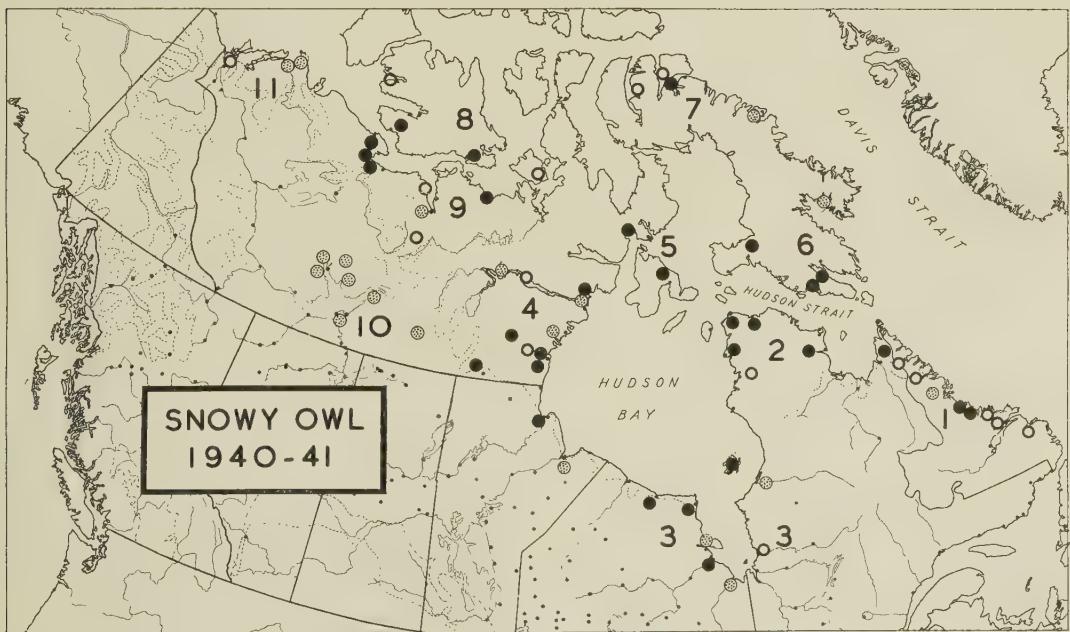
Fig. 4.

Figs. 3, 4. Reports about the lemming and snowy owl populations in 1940–1 compared with 1939–40. Each symbol is at the approximate centre of an observer's area: solid black discs are INCREASE; plain circles are DECREASE; circles with small dots are NO CHANGE, NOT ABUNDANT; circles with larger, irregular dots are NO CHANGE, ABUNDANT.

supposing that the end of the cycle had been passed. All reports agree that foxes were increasing.

Chesterfield Inlet. 'No white lemmings were seen. The brown species was seen in far the largest numbers during the spring months of 1941, but from the reports of natives they were less abundant than in the previous year. During the winter very few signs were seen on top of the snow.' (L. E. Corey.)

Fort Ross, King William and Victoria Islands (group 8). In 1939-40 lemmings either reached the bottom of their cycle or, at Fort Ross and King William Island, had already done so the previous year. In 1940–1 a good recovery was reported from Victoria Island but none was evident near the posts of Fort Ross or King William Island, though some abundance was reported inland from the latter. Snowy owls made the beginnings of a recovery while foxes showed a marked improvement which was shared by Fort Ross later in the spring.

King William Island. 'White foxes, lemming and snowy owls very scarce during fall and early winter months. There was a small migration in February.... No snowfall in the fall and early winter seemed to have kept lemming and foxes away from this locality as the land, being bare, afforded no shelter to lemming. It was noted, however, that most of the foxes caught were fat and had been feeding inland as no seal blubber on their fur. Some fox signs were noticed in April which seems to indicate that foxes will be more plentiful next season as there were no fur signs here the previous April.' (W. F. Joss.)

Cambridge Bay. 'From native reports lemmings have been abundant winter months inland. Natives coming from inland (mainland) had good fox catches, local natives trapping in this vicinity had practically nil. Snowy owls, lemmings and foxes were unusually scarce until late spring.' (E. J. Gall.)

Read Island. 'White foxes were fairly plentiful all winter, but though thin they refused to consider bait of any kind. About March the first foxes were taking bait more readily, but these foxes were very fat and the fur on a very large percentage of them was badly rubbed—some of them so badly as to be valueless.

'I have heard a theory expressed that these rubbed foxes migrated from the south but I understand that the fur that came in from south of Coppermine and Kugaryuak was of an exceptionally good quality. My theory is that they came from the north, because natives to the west and north of here caught the rubbed foxes a week or so before the natives to the east and south started catching them; and also because natives on Banks Land and Walker Bay districts had good hunts for the whole of the trapping season. Around here practically no foxes were either seen or caught along the coast, nor were any tracks observed on the ice.

'Lemming were exceptionally abundant during the season and nothing unusual has been reported about them except that many dead baby mice were observed in the nests when the snow disappeared. Some nests had only one, while others were observed with three dead ones. Young mice were exceptionally abundant around here when the snow was melting.

'Snowy owls were abundant last fall up till about Christmas when they disappeared during the cold short days, but appeared again in March.' (F. R. Ross.)

Holman Island. 'According to reports there was a heavy migration of white fox across the Prince of Wales Straits from Banks Island into the Walker Bay and Minto Inlet area during March, April and May. Some of these foxes were trapped during March and it was noticed that most of the pelts were very small and a lot were not in very good condition. They had very little hair on their backs and tails, what hair there was, was very short and blue in a long oval patch from neck to hindquarters. Some had no hair on the necks and the appearance was as if they had been continually scratching the hair out. In nearly all cases the hair on the bellies was in good condition.' (H. W. Chitty.)

3. CHANGES IN THE MAINLAND POPULATIONS, BAKER LAKE AND WEST: GROUPS 4, 9–11

(a) Lemmings

In the regions discussed in § 2 the existence of a short-period fluctuation in lemmings, arctic foxes and snowy owls is well established by the questionnaire replies; but about the area north of the timber line between Baker Lake and Alaska the information does not give such a clear-cut picture. This area has been little visited by zoologists and our knowledge is very limited as to species, range, abundance and relative importance as fox food of the various small mammals. No published evidence exists to show the likelihood of cycles in wild life comparable with those in the Eastern Arctic (Hewitt, 1921 (largely Eastern Arctic fur returns); Elton, 1931, 1934, 1942). Recently, Clarke (1940) has contributed a wealth of information about the barren lands of the interior and several passages from his admirable account are relevant to the present discussion:

'To what extent the fluctuations of animals dwelling in the interior barrens-eastern Great Slave Lake region conform to the ideas of periodicity that have grown up in the last few years is hard to say. They certainly fluctuate in a manner typical of the familiar cycles, but evidence is lacking as to whether the periods of the cycles are identical, and, conditions being vastly different from those in other parts of the country, it is at least possible that they are not' (p. 64).

'The consensus of opinion in the Reliance area is that the fox-lemming relationship does not hold in a place like Artillery Lake where caribou (and wolves) are common in winter. Some trappers are willing to admit that it might hold in places not in the winter range of caribou, but many of them "don't believe in it"' (p. 67).

The difficulty of sifting the evidence provided by the enquiry about lemming numbers is complicated to some extent by the presence of other species of small rodents. It is difficult to know how many of the observers are correct in their identifications when they give separate estimates for lemmings and mice: especially as many reports about lemmings received from areas well inside the timber line prove that here, at least, the distinctions are not clear. It is not, however, easy to reject all such reports because, particularly in group 10, the information often comes through travellers from the barren lands. Notes on the small rodent species based on Anderson (1934, 1937) were given in the 1935–6 report. The following summary repeats some of these notes with added information from Anderson (1937) and Clarke (1940):

Back lemming (Lemmus trimucronatus trimucronatus). This lemming, which stays brown all year, occurs on the barren ground from Hudson Bay to the eastern edge of the Mackenzie River delta and south to Artillery Lake and Thelon River.

Alaska brown lemming (Lemmus trimucronatus alascensis). Occurs west from the delta to north-west Alaska.

Richardson collared lemming (Dicrostonyx groenlandicus richardsoni). This species, which turns white in winter, is found on Hudson Bay north from Churchill and from the Thelon Game Sanctuary to Bathurst Inlet. Clarke obtained specimens from Clinton Colden, Heuss and Baker Lakes.

White lemming (Dicrostonyx groenlandicus rubricatus). Ranges east from Coronation Gulf to northern Alaska. 'A common belief among the Eskimos is that the White Lemmings fall from the sky in winter.... The explanation is that...they are seldom seen in winter except when a blizzard removes the snow above their runways. In summer most of the natives do not distinguish the lemmings from other mice' (Anderson, 1937).

Barren ground meadow mouse (Microtus pennsylvanicus aphorodemus). Occurs on the west coast of Hudson Bay, but its limits are quite unknown. It undoubtedly contributes to the food of the fur bearers.

Drummond meadow mouse (*Microtus pennsylvanicus drummondii*). Its range is from the prairie provinces north to the tree limit and beyond—to within 20 miles of Franklin Bay. Clarke obtained it at Clinton Colden and Artillery Lakes and midway down the Thelon River. At Churchill it intergrades with *M. p. aphorodemus*.

Macfarlane tundra mouse (*Microtus operarius macfarlani*). Specimens are available from Firth River (near the north-east border of Alaska) to Langton Bay where Anderson found it abundant in 1910 and 1911; he says: 'The tundra mouse is often abundant and is a prey of the Arctic fox.'

Two other species which extend their range beyond the timber line are *Microtus xanthognathus*, found ocally from central Alberta north to the Arctic coast and west to central Alaska, and *Clethrionomys dawsoni dawsoni* taken by Anderson on Coronation Gulf and by Clarke at Crystal Island in Artillery Lake, Thelon River and Baker Lake.

Information about lemmings and 'mice', omitting all reports from inside the timber line, have been reassembled into smaller regional groups in Table 4, the data being taken from Table 1 for each year.

Baker Lake. In 1937 Clarke found lemmings scarce, but their signs abundant, and was told they had died off in the spring of 1937—which disagrees with the *decrease* already reported for 1935–6 in answer to the questionnaire. Farther west:

'In the Beverly-Aberdeen Lakes region there were plenty of runways; in some spots lemmings seemed to be still abundant, in others they were gone and the occasional body on the ground placed the dying off in the winter of 1936–37 or the spring of 1937. On the shore of Aberdeen Lake there were literally windrows of lemming "seeds" (coproids).' (Clarke, 1940, p. 67.)

After this disappearance some time in 1935–7 no recovery was reported before 1940–1 except in mice during the previous year.

Adelaide Peninsula to Bathurst Inlet. For no part of this coast is there a continuous series of records for the six years of this study. It is probable, however, that between Adelaide and Kent Peninsulas lemmings increased during 1936–8 up to a considerable density and declined some time during 1938. According to a report already quoted from E. Parsley at Cambridge Bay, a migration north from the mainland was observed by the post manager at King William Island in May 1937. J. U. Eddy also reported many lemming tracks on the ice off the mainland between King William and Victoria Islands (March, May 1937). A fuller account of lemming abundance was given by A. Gavin in the *Winnipeg Free Press*, 2 May 1942 (we are indebted to Mr R. A. Gibson for sending us a clipping). No year is given, but the context makes it certain (Anon, 1937) that the account refers to 1937:

'...I was camped at the old post site at the mouth of the Perry river. The new post was to be opened on Flagstaff Island, 12 miles out in Queen Maud sea, where navigation was not so complicated.

'For four days I checked and loaded stores for transport by sled to the new post. Each day the lemmings became more numerous. The tundra was alive with them. On the fourth day I started north with a full load.

'I soon realized that I was cutting through a mass migration of lemmings. They were everywhere on the sea ice, all travelling due east. As far as the eye could see in any direction, the lemmings were on the march. It was the first of May, and pools of water covered the sea ice.

'Open leads, 10 to 20 feet wide, gashed the ice. But the lemmings stopped for nothing. They never hesitated, but plunged from the ice edge to the water a foot below and swam across. On the other side, they tried vainly to climb the sheer wall of ice. Thousands drowned, but they came on in never-ending numbers....

'I estimated that the average density was one lemming to every square yard. Later enquiries from the Eskimos revealed that the mass migration was going on at the same time at the Kogyuak River, 45 miles east and for at least 15 miles west of the post. The peak was reached on May third and fourth and

Photo D. Chitty

Photo 1. A typical settlement in the Subarctic: Lake Harbour, southern Baffin Island. The buildings belong to the Anglican Mission and Hudson's Bay Company; those of the Royal Canadian Mounted Police are up the inlet behind the hill. 15 August 1939.

Photo A. F. Sherzer

Photo 2. Eskimo summer camp on the tundra at Chesterfield Inlet, 10 August 1939. The tent in the foreground is partly made from skins (seal, dog, wolf, etc.).

Photo A. F. Sherzer

Photo 3. Pangnirtung Fjord from Mt Duval (2250 ft) near the settlement, 13 September 1939. "The eastern coastline [of Baffin Island] is generally high and rocky, with many deep inlets and bays." *Canada's Eastern Arctic* (1934).

Photo A. F. Sherzer

Photo 4. Craig Harbour, southern Ellesmere Island, 22 August 1939. Until 1940 two men of the Royal Canadian Mounted Police were stationed here. Navigation is only possible for a few days each year.

gradually tapered off and ceased about the seventh. From start to finish, the movement lasted for 10 days.'

For 1937–8 there was one report of *no change* in the Adelaide Peninsula (but snowy owls: *increase, abundant*) and two reports of *increase, abundant* in the Kent Peninsula. The year following A. Gavin reported *decrease* and scarcity at Perry River.

There is only one report for 1939–40, and this stated that some increase had occurred at Sherman Inlet, Adelaide Peninsula, with decrease and scarcity elsewhere from Back River to Kent Peninsula.

In 1940–1 three observers (at Perry River, Kent Peninsula and Arctic Sound in Bathurst Inlet) reported increase and abundance. The post manager at Bathurst Inlet reported no change in lemmings but that mice had remained abundant. The lemming story at this post from 1935 to 1941 is quite obscure, and apart from the information in Table 4, the only remarks about lemmings were for 1935–6:

'Lemming, while not what one would call abundant, are very plentiful for Bathurst Inlet. Wild mice very plentiful and still are, July 15 1936.'

From this available evidence it seems that lemmings were at a considerable peak in the area Adelaide Peninsula, Perry River, Kent Peninsula during 1937. Sometime in 1938 the lemmings 'crashed', to recover again by 1940–1.

Barren lands between Bathurst Inlet and Great Slave Lake. Reports from any one locality in this area are incomplete and hard to interpret. In the north (Beechey Lake, etc.) there were signs of increase, and some abundance, in four of the six years for which there are records and news of a great migration at Muskox Lake in April 1940 reached Reliance (R. W. Thompson, see report for 1939–40). G. D. de Steffany reported increase and abundance in 1937–8 at Lakes Providence and de Gras, and in 1938–9 stated for Lac de Gras to Fry Lake: 'Lemmings have been on the increase for several years.' At Aylmer Lake no special abundance was noted in the years covered by reports. At Clinton Colden, Ptarmigan and Artillery Lakes voles, mice and lemmings were scarce in the summers of 1936 and 1937 (Clarke, 1940) and no striking recovery has been reported since, though R. W. Thompson states:

'Was informed they migrated eastward during April 1941 across Ptarmigan Lake and that they were very ferocious: would stand on their hind legs and wave their paws if molested by dogs.'

Round the headwaters of the Hanbury and Thelon Rivers lemmings had evidently been abundant in 1935 in some areas and in 1936 in others; while in 1936–7 a migration over the ice of Whitefish Lake was reported to the police at Reliance (Clarke, 1940, p. 67).

These data, like those from Bathurst Inlet, reveal differences in abundance but not the existence of any obvious short-term fluctuation in small rodents.

Coppermine to Stapylton Bay. In 1935–6 there were three contradictory reports about lemmings:

'There seem to be more lemmings than I have seen around Coppermine for many years this last month (May).' (J. H. Webster.)
'Not many lemmings are seen near the settlement but there were an unusual number of mice this spring.' (D. E. Parkes.)
'Lemmings less—scarce. Mice less.' (C. Reiach.)

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From later reports it is evident that lemming numbers remained fairly low until, in the late winter 1939 (see last report) and again in September 1940, increases in numbers were evident:

58. 'Never saw so many lemmings before: they migrated here 20–25 September.' (J. H. Webster.)

32. 'More lemming in this district during past year than have been known for many years. Very few noticed during winter; but reports that foxes were unwilling to take bait from traps indicate that many were under the snow. A few dead lemmings noticed when snow cleared in spring.' (R. N. Yeats.)

24. 'Brown lemming are here for the first time in 13 years and unusually abundant. White lemming very plentiful but not as many as other species.' (L. F. Semmler.)

'Mr W. Storr, trapper of Stapylton Bay, reported that last fall (1940) a great number of lemming came down to the beach and without hesitation walked over the ice along the beach and jumped or walked into the water and started to swim. Many drowned when exhausted while others crawled out on to floating ice and died.' (F. R. Ross.)

Towards Great Bear Lake abundance of lemmings or 'mice' was reported in 1937–9.

Pearce Point to Alaska. From Baillie Island a good account was received of lemmings in considerable abundance in May 1937 (see 1936–7 report). A decline set in in the spring of 1938, and since that year there had been no recovery. In the Mackenzie delta there was some abundance in 1937–8 and once again in 1940–1. Recent information is lacking from west of the delta.

Summary. There is some evidence for thinking there may be a short cycle in lemming numbers on the coast between Adelaide and Kent Peninsulas. To the west and south-west of here the data have not so far revealed a similar short periodicity; but unfortunately the reports do not form an uninterrupted series.

The complexity of ecological interrelations in the area may mean that the study of fluctuations by the questionnaire method breaks down. There is need, in any case, for these vital problems to receive permanent study by biologists in the field.

(b) *Arctic fox and snowy owl*

'At Baker Lake the arctic fox is the only significant fur-bearing animal. There in recent years, the short cycle has been indicated, 1930–1 and 1933–4 being peak years. At Snowdrift 1931–2, 1933–4, and 1934–5 have been recent peaks, indicating a similar cycle. The peaks there are not high, there being always caribou around Snowdrift, so that, with foxes following the caribou, there may be little difference from year to year in the catches of the top men. In good years foxes are everywhere, and no one misses out on them, but in bad years some trappers may not see a fox. This exception may be noted, namely, that 1936–7 was a real low year, with foxes unmistakably scarce.' (Clarke, 1940, p. 66.)

Following this universally bad year came a year of recovery, then one of general abundance (1938–9) from Bathurst Inlet south through the barren lands to Snowdrift. There was a sharp decline in 1939–40 followed by recovery in 1940–1. Although these changes suggest that, as in the eastern Arctic, a short cycle is operating in arctic fox, it cannot, as already shown, be correlated with any lemming cycle yet apparent from the enquiry. For Baker Lake there is evidence from earlier years that it shares the eastern Arctic fox cycle (Elton, 1931). Its most recent peak was either 1937–8 (I. ×) or 1938–9 (N. ×).

Little increase and no great abundance was reported along the coast in any of the five years before 1940, and the increase in 1940–1 seems to have been less pronounced than throughout the interior barren lands.

9. *Muskox, Beechey, Fry Lakes.* 'Last season's catch was ten white fox as compared with 552 this season.' (M. P. Murphy.)

Snowy owls, with few local exceptions, seem to have been rare throughout the whole area and no broad regional trends can be detected during 1935–41.

33. *Baker Lake.* 'Snowy owls seldom frequent this district: have seen only one during past year.' (H. A. McBeth.)

4. SLEDGE DOGS

From Churchill up the west coast of Hudson Bay and from Coppermine up the west coast of Victoria Island teams have been severely hit by 'distemper', apparently spread by contact between teams. Some of these same teams suffered as recently as 1938–9, and the prevention of their periodic decimation remains one of the problems most vitally needing a solution. The epidemics which have broken out during the six years of this study do not seem to have originated from disease in wild life: 'crazy disease' has been notably absent.

5. METHODS

In the present paper the areas have not, as hitherto, been fully plotted from the descriptions in Table 1. Instead, one symbol has been used for each report and placed as far as possible in the centre of the area. As there are so few observers at any one place, it has been possible without departing far from this rule to avoid overlapping any of the symbols. Instead of a series of upright arrows, a black disc shows the general location of an *increase* report; white is used for *decrease*, small dots for *no change, not abundant*, and larger, irregular dots for *no change, abundant*. The contrast between these symbols is greater than it was with the arrows and the greater simplicity in reading, as well as constructing the maps, compensates for the omission of the full area covered—which may still be found from Table 1.

6. ACKNOWLEDGEMENTS

7. SUMMARY

1. Answers to seventy-nine questionnaires showed that 1940–1 was a year of almost universal increase in arctic foxes throughout the Arctic and Subarctic.

2. In the Eastern Arctic (north of 60° N. lat.) this improvement followed a year in which lemmings and snowy owls had started their recovery from the bottom of the previous cycle. This recovery was continued throughout 1940–1.

3. On the Western Arctic mainland no general correlation of fox, lemming and snowy

owl fluctuations was revealed from an analysis of the data for 1935–41, and only in the arctic fox in the interior barren lands was there evidence of a short-period cycle.

4. Sledge dogs have not suffered widespread epidemics; but on the west coast of Hudson Bay and north from Coppermine 'distemper' was spread by contact between teams.

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Appendices

Table 1. *Summary of observers' statements about arctic fox, lemming, 'mice', snowy owl and sledge dog (part) for 1940–1*

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, a. = abundant, × = neither.

Sledge dogs: 0 = disease reported absent. 0* = slight disease or starvation reported, + = more serious disease; details in Table 3.

Square brackets indicate observations that have been partly or entirely omitted from map or Table 2: (1) parts or all of some areas are not mapped if they are certainly outside the animal's range; (2) in groups 2 and 3 reports from inland posts are not mapped or included in Table 2; (3) reports on 'mice' and events at special times of the year are not included in the maps or in Table 2.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire Unnumbered replies were received from the Hudson's Bay Company.

	Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
Group 1. Northern Labrador coast					
Cartwright, half-way both to Frenchman's Island and Rigolet and 80 miles inland. (R. M. Howell)...	D. s.	—	I. a.	D. s.	0
Rigolet, south 50, north 75, west 35 miles. (G. Budgell)	D. s.	none	D. s.	D. ×	0*
Northwest River [and inland 500 miles]. (J. E. Keats)	none	—	D. s.	—	+
Makkovik, 50 miles north and south [and inland, north and north-west, 100 miles from post]. (H. Leaman)	D. s.	D. s.	D. s.	D. s.	+
Hopedale and 30 miles radius. (S. E. Dawe) ...	D. s.	—	N. ×	I. ×	—
Davis Inlet and 30 miles radius. (W. R. Bull)	D. s.	—	D. s.	I. a.	0
Nain, north 35, south 30 miles; west and north-west 75 miles; coastal islands. (J. F. Delaney)... ...	D. s.	N. ×	N. ×	N. ×	0
{Nutak and 25–35 miles radius. (D. W. Massie) ...	—.	I. ×	I. a.	D. s.	0*
{Also 100 miles west	D. s.	—	—	—	—
{Hebron; 50 miles south and inland 150 miles; 180 miles north and inland 200 miles. (T. Budgell) ...	I. ×	I. a.	I. a.	D. s.	0

Table 1 (continued)

	Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
Group 2. Coast of Northern Quebec, south to Richmond Gulf [and inland]					
Georges River, south-west 50 [to 100] miles, east to coast, north-east to Port Burwell. (J. A. Ford) ...	N. s.	I. ×	I. ×	I. ×	+
[Fort MacKenzie and 120 miles radius.] (C. N. Stephen)	[D. s.]	[N. s.]	I. ×	—	—
Payne Bay and 300 sq. miles. (L. Coates)	—	I. a.	N. ×	I. a.	0*
Inland	I. ×	—	—	—	—
Sugluk; Wakeham Bay to Kovik River [and radius of 100 miles inland]. (M. L. Manning)	I. a.	I. a.	—	I. a.	0
Wolstenholme; east to within 20 miles of Sugluk, south 72 miles to Kovik River. (F. Melton) ...	I. a.	I. a.	I. a.	I. ×	0
Cape Smith, inland 50, south to Magnet Point and north to Kovik Bay. (P. A. C. Nichols)	I. a.	I. a.	I. ×	I. a.	—
Along coast	s.	—	—	—	—
Povungnetuk; north to Magnet Point and south to Mistake Bay [inland to Long. 75°]. (R. Cruickshank)	I. a.	I. a.	D. ×	D. ×	0
Group 3. South parts of Hudson Bay, James Bay [and inland]					
Belcher Islands. (E. H. Riddell)	I. ×	I. a.	—	I. ×	0
Great Whale River, north to Richmond Gulf and south to Cape Jones [inland 100 miles]. (T. C. Carmichael)	N. s.	D. s.	D. s.	N.	0
Fort George and 100 sq. miles. (R. M. Duncan) ...	D. s.	—	N. ×	—	0
Kanaapuscow and 50 sq. miles. (W. R. Kell) ...	—	—	N. ×	—	0
[Nitchequon...and west 100 miles.] (D. E. Cooter)...	[N. s.]	none	N. ×	none	0
Eastmain, north 50, south 20 [inland 200 miles] ...	D. s.	none	D. s.	D. ×	0
Moose Factory and 40 miles radius. (W. T. Watt)	—	—	I. ×	N. s.	0
Moosonee and 50 miles radius	—	—	N. s.	—	0
Albany and 35 miles radius. (W. B. Anderson) ...	none	none	I. a.	I. s.	0
Attawapiskat, south to the Lawashi River [150] miles inland, north to the Ekwan River. Also Agamiski Island. (A. W. Michell)	N. ×	—	I. ×	N. s.	—
Lake River and 75 miles radius. (R. C. Ross) ...	N.	×	I.	I.	0
Weenusk, north 70, south 50, inland on Weenusk River [150 miles]. (T. K. Griffin)	D. s.	—	I. a.	I. ×	—
York Factory and 50 miles radius. (H. F. Blade) ...	D.	none	I. a.	N.	0
Group 4. West coast of Hudson Bay, north from Nelson River and inland					
Churchill to Cape Churchill [north to Long Point] and west 50 miles. (A. B. Urquhart)	none	—	N.	I.	+
Nueltin Lake and south to Manitoba border, west to Kasba Lake, north to north end of Ennadai Lake, east to north end of Nueltin Lake and down west coast. (J. A. Trafford)	I. a.	I. ×	—	I. ×	0*
(10) Eskimo Point, north 40, south 50–70, west 90 miles. (W. C. Brownie)	I. a.	I. a.	I. a.	I. ×	+
5. Eskimo Point to Padley. (H. P. Dionne)	I.	I. a.	—	D. s.	+
November, December	a.	—	—	—	—
Spring	[D.]	[D.]	—	—	—
34. Eskimo Point, south to Nonala, west to Padley, north along coast to Tavane. (H. O. Humphrey)	—	D. s.	—	—	—
Eskimo Point vicinity...	I. a.	—	—	I. a.	+
Padley and 20 miles radius. (D. Drysdale)... ...	I. ×	I. ×	I. a.	I. s.	+
Tavane, north to north end of Yathkyed Lake, then north-east to north end of Kaminuriak Lake, then east to Rankin Inlet, then south down Hudson Bay coast to Maguse River. (G. Anderson)	I. a.	N. ×	—	N. ×	+
Chesterfield Inlet to Daly Bay; south to Marble Island and 60 miles inland. (J. L. Ford)	I. ×	I. a.	—	N. ×	+
35. Chesterfield Inlet, south to Mistake Bay, north to Wager Bay. (L. E. Corey)	I. a.	D. ×	—	I. a.	—
Late fall and winter	—	—	—	[D.]	—
Wager Bay, April	—	—	—	none	—
Mistake Bay to Cape Fullerton	—	—	—	—	+
Baker Lake [and 150 miles radius]. (A. Lunan) ...	I.	D. ×	—	D. s.	0
33. Baker Lake to Beverley Lake and Lat. 64–65°. (H. A. McBeth)	I. a.	I. a.	—	N. ×	0
Winter and spring	[D.]	[D. s.]	—	—	—

Table 1 (*continued*)

	Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
Repulse Bay and 20 miles radius. (T. Crawford) ...	I. ×	I. ×	—	I. ×	0
Southampton Island, except coastline, from Duke of York Bay to East Bay. (P. Dalrymple) ...	I. a.	I. a.	I. a.	I. ×	0
Group 6. Southern Baffin Island					
Lake Harbour, from Robinson Sound and Frobisher Bay to south coast of Baffin Island, west to Markham Bay. (J. Bell) ...	I. ×	I. a.	—	I. a.	0
Coast ...	s.	—	—	—	- -
36. Lake Harbour; Amadjuak east along coast to Gabriel Strait, and all Frobisher Bay to Cape Haven. (D. P. McLaughlan) ...	I. ×	I.	—	I. a.	0
Spring ...	[D.]	a.	—	—	—
Cape Dorset and Foxe Peninsula south and west of Koukdjuak River, Nettiling Lake, Amadjuak River and Lake. (O. M. Demment) ...	I. ×	I. a.	—	I. ×	0
Pangnirtung, Cumberland Sound and 10 miles inland. (J. A. Thom) ...	N. s.	I. ×	—	N. ×	0
Late April and early May ...	[I.]	—	—	—	—
Group 7. Northern Baffin Island, and north. Also Igloolik					
Clyde River to Coutts Inlet and Home Bay. (J. G. Cormack) ...	I. ×	I. ×	—	N. s.	0*
Pond Inlet, Eclipse Sound and Navy Board Inlet. (A. T. Swaffield) ...	N. ×	N. a.	—	D. s.	0
37. Pond Inlet, Eclipse Sound, Milne Inlet and Navy Board Inlet. (T. T. Birkett) ...	N.	N. a.	—	I. a.	0
Arctic Bay, all of Admiralty Inlet and Bernier and Agu Bays. (T. Ross) ...	I. ×	I. a.	—	D. s.	0
Group 8. Boothia Peninsula and Islands west and north					
Fort Ross, north to Port Leopold, south to Lord Mayor Bay and west to Prince of Wales Island. (W. A. Heslop) ...	D. s.	D. ×	—	—	0
After 31 March ...	[I. a.]	—	—	—	—
(1) King William Island: Petersen Bay–Gjoa Haven Vicinity. (W. F. Joss) ...	I. ×	D. s.	—	D. s.	—
Inland, November ...	—	a.	—	—	—
Petersen Bay to Terror Bay and (Group 9) Back River to Adelaide Peninsula ...	—	—	—	—	0
(26) Cambridge Bay and 50 to 100 miles radius (including Kent Peninsula, Group 9). (E. J. Gall) ...	s.	s.	s.	s.	—
Late spring ...	I. a.	I. a.	I. a.	I. a.	—
Inland, winter ...	a.	a.	—	—	—
Read Island; Lady Franklin Point, west along coast to Cape Baring, east to extreme east end of Prince Albert Sound, back overland. (F. R. Ross) ...	I. a.	I. a.	—	I. a.	-
Christmas to March ...	—	—	—	s.	—
Holman Island from Investigator Island in Prince Albert Sound to Minto Inlet and Deans Dundas Bay. (H. W. Chitty) ...	I. ×	I. a.	—	D. ×	—
Group 9. Pelly Bay, west to east of Coppermine River					
Perry River and 60 miles radius. (A. Gavin) ...	I. a.	I. a.	—	I. a.	0
Bathurst Inlet, north to Burnside River, and west from foot of Inlet 150 miles ...	—	N. ×	N. a.	N. ×	—
Arctic Sound. (I. Leonard) ...	I. ×	I. a.	—	D. ×	0
9. Muskox, Beechey and Fry Lakes. (M. P. Murphy)	I. a.	I. a.	a.	D. ×	—
Fort Reliance ...	—	—	—	—	—
Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
Fond du Lac: north towards Wholdaia Lake. (G. E. Duncan) ...	I. a.	—	—	N. ×	0
Stony Rapids [west 25, south 20, east 90] and north 300 miles. (W. S. Carson) ...	I. a.	N. ×	I. ×	N. ×	0

Table 1 (continued)

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
30.	Reliance district, Lat. 62–64°, Long. 106–110°. (R. W. Thompson)	I. a.	N. ×	—	none	0
27.	Artillery, Ptarmigan and Clinton Colden Lakes. (A. J. Knox)	I.	I. a.		none	+
	Fall	a.	—	—	—	—
	Snowdrift and 200 miles radius. (M. C. Watson) ...	I. a.	I. a.	I. ×	N. ×	0
23.	Snowdrift River, Nonacho Lake and Taltson River. (W. H. Haywood)	I.	s.	D. s.	s.	0
	Barren lands to the north	a.	—	—	—	—
	Fort Resolution and 50 miles radius. (W. M. S. Skinner)	—	[N. ×]	N. ×	N. ×	0
	May	—	[I.]	[I.]	—	—
	Barren lands east of Reliance	I. a.	—	—	—	—
15.	North arm of Great Slave Lake from Rae north-west to Marten Lake and an area north-east of about 100 miles. (A. T. Rivett)	—	none	→	N.	..
	Barren lands north of Rae, Winter Lake area and north end of Snare Lake	I.	—	—	—	—
	North arm of Great Slave Lake and 100 miles radius	—	—	—	—	0
7.	Fort Rae, and west shore of Marion Lake, Duport River and south-west 60 miles. (F. D. Riley) ...	none	[D. s.]	—	N. s.	—
	Fort Rae and Yellowknife vicinity	—	—	—	—	0
	Fort Rae, south-east 80, north and north-east 150 [north-west 150 and north-north-west 180 miles]. (R. Middleton)	I. ×	N. a.	N. a.	N. s.	0
	Yellowknife; Lat. 62–63°, Long. 112–116°. (T. Scurfield)	I.	I. a.	I.	N. ×	0
	In Barren lands	a.	—	—	—	—

Group 11. Coppermine River to Alaska

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
28.	Coppermine Settlement and 4 miles radius. (J. H. Webster)	—	I. a.	—	—	..
	Coppermine Settlement to Bloody Falls ...	N. s.	—	—	I. a.	—
32.	Mouth of Coppermine River, west up Richardson River, north to Krusenstern and Stapylton Bay. (R. N. Yates)	—	I. a.	—	—	—
	Coppermine River, Kugaruak River and inland, Stapylton Bay, Bernard Harbour, Krusenstern ...	—	—	—	I. a.	—
	Late winter	—	—	—	[D. s.]	—
	As above, and (Group 8) Lady Franklin Point ...	I. ×	—	—	—	—
	As above, and (Group 8) Read Island and Prince Albert Sound ...	—	—	—	—	r
24.	Krusenstern district west to Stapylton Bay and 40 miles up Rae River. (L. F. Semmler)	I. ×	I. a.	—	I. a.	—
	Krusenstern district	—	—	—	—	0
	Stapylton Bay. (W. Storr per F. R. Ross)	—	a.	—	—	—
13.	Anderson River west 15 miles to Nicholson Island, north 60 miles to Baillie Island. (S. Mason) ...	I. ×	D. s.	—	N. s.	0
	Maitland Point, north to Baillie Island, east to Horton River, south to Anderson River, west to Nicholson Island	I. ×	D. ×	D. ×	N. ×	-
(11)	Tuktuk, north to Cape Dalhousie, east to Huskie Lakes, west to west side of Richards Island, south to Kittigazuit [and Tununik]. (J. E. Sidgwick) ...	D. s.	D. ×	I. ×	×	0
	Fall until sea froze over	a.	—	—	—	—
21.	Arctic Red River to Thunder River. (W. D. Clark)	none	none	a.	[N. ×]	0*
4.	Arctic Red River and 50–80 miles radius. (J. Nagle)	[N.]	[D.]	—	[N.]	0
	Arctic coast	s.	a.	—	—	—
8.	Point Separation. (E. Larson)	none	a.	—	none	0*
3.	Aklavik Reindeer Reserve and MacKenzie River delta. (J. A. Parsons)	I.	—	—	D.	—
	Reindeer Reserve to Aklavik	—	I.	—	—	—
	Reindeer Reserve	—	—	—	—	0
14.	Aklavik to coast, lower MacKenzie delta. (E. S. Covell)	I. ×	none	I. a.	none	0

Table 2. *State of arctic fox, lemming and snowy owl populations in 1940–1.*
Number of observers reporting relative abundance compared with 1939–40

Group no. ...	Eastern Arctic									Western Arctic					
	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	1	5	1	10	2	3	2	24	**57**	4	3	10	6	23	**88**
Decrease	7	—	4	—	—	—	—	11	**26**	1	—	—	1	2	**8**
No change	—	1	3	—	—	1	2	7	**17**	—	—	—	1	1	**4**
Total	8	6	8	10	2	4	4	42	**100**	5	3	10	8	26	**100**
Lemming:															
Increase	2	6	1	6	2	4	2	23	**72**	3	3	3	4	13	**59**
Decrease	1	—	1	3	—	—	—	5	**16**	2	—	—	3	5	**23**
No change	1	—	—	1	—	—	2	4	**12**	—	1	3	—	4	**18**
Total	4	6	2	10	2	4	4	32	**100**	5	4	6	7	22	**100**
Snowy owl:															
Increase	2	·5	4	6	2	3	1	23	**52**	2	1	—	3	6	**28**
Decrease	5	1	1	2	—	—	2	11	**25**	2	2	—	1	5	**24**
No change	1	—	4	3	—	1	1	10	**23**	—	1	7	2	10	**48**
Total	8	6	9	11	2	4	4	44	**100**	4	4	7	6	21	**100**

Table 3. *Information about sledge dogs, 1940–1*

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company. Reports of serious disease are marked + in this table and shown by a black disc on the map. Outbreaks apparently less serious, deaths through starvation, etc. are shown by a broken circle on the map. Absence of trouble is shown by a full circle; but names of these posts, other than those given in Table 1, are not listed. Not more than one symbol is given for each report except where indicated (2 + etc.). Fuller descriptions of some of the areas are in Table 1.

Quebec and Labrador

+   *Seven Islands.* 'Disease began in December 1940, origin unknown. Symptoms were semi-paralysis of hind-quarters, discharge from nostrils and eyes, intermittent internal spasmodic pain. About 15–20% of all dogs were affected, and of these almost all died. No treatment attempted.' (G. A. S.)

+   *St Augustin.* 'Outbreaks of disease continued from last year, in no particular month, just happening any time. Nothing definite about origin. Contracted along coast, first being noticed at Harrington last year, then spread eastward. Some fell dead, others pined away, had paralysis of hind-quarters, runny eyes, stoppage of bowels and loss of all hair, leaving bare skin. Approximately 40 dogs, maybe more, were affected this year, many last year. About 15 died this year. No treatment attempted, more than sulphur or gunpowder in feed.' (B. G. C.)

     Rigolet. 'Some dogs suffered from loss of strength in their hind legs. We did not hear of any deaths resulting from this disease, except for the fact that some were shot by their owners. We think the disease was caused by lack of food, as dogs which were fairly well fed escaped the disease.' (G. B.)

+   *Northwest River.* 'Disease began in March, origin unknown. The symptoms were frothing at mouth, but not mad, vomiting, diarrhoea, passing blood, no appetite. Probably about one-half of the dogs were affected, and a few died. The observer is not aware of any treatment having been attempted.' (J. E. K.)

+   *Makkovik.* 'Disease began in January, origin unknown. Dogs got weak on the legs and some lay down and died, while others survived the disease. Approximately 50 dogs were affected and approximately 20 died. No treatment, except that some were given sulphur.' (H. L.)

     Nutak. 'There have been, during the winter, several apparent cases of disease, but this, we think, is entirely attributable to lack of suitable food, and not to any other cause. A considerable number of native dogs have, it is true, died during the winter, but this was due to starvation, although, in some cases, just before death, symptoms were evident which are generally associated with some types of disease.' (D. W. M.)

+   *Georges River.* 'Occasional outbreaks of disease among sledge dogs have occurred from November 1940 and throughout the winter. Only about 12 dogs have died but quite a number were affected and seem to be recovering. Symptoms were various: some with tape worms, others with skin disease causing a well-fed, well-furred dog to lose all its fur within a week to 10 days. Others seem to be affected in the rump and still others either in the head or neck.' (J. A. F.)

     Payne Bay. 'There was a slight sickness among some of the dogs in February and March. The dogs would not eat even fresh seal meat during the sick spell, but very few dogs died directly due to the sickness. There were a lot of deaths but it was due to starvation.' (L. C.)

+   *Barrière.* 'Disease began in April, origin unknown. Symptoms were loss of weight, matter in eyes and nose, "dizzy" spells. About 25 were affected and 10 died. Treatments attempted were Dr Bell's Distemper Remedy and "Nema" worm capsules.' (W. A. W.)

Table 3 (continued)

+ *Obijuan.* 'Disease occurred in October and November, origin unknown. Symptoms were vomiting and dragging of the hind-quarters, frothing at the mouth, when dying. Between 20 and 30 dogs were affected, and about 20 died. Very few survived. No treatment attempted.' (F.McL.)

Manitoba

+ *Poplar River.* 'Disease began in February. Dogs got tape and kidney worms from feeding on fresh fish. They tired early after exertion and gradually wasted away. About 12 dogs were affected, and all died. No treatment was attempted.' (C.A.N.)

+ *Split Lake.* 'Disease began in December, originated from camp up from south. Symptoms were distemper with pneumonia. Fully 70% were affected and fully 40% died. Treatment was attempted.' (A.M.)

Gillam. 'Disease began in February, origin unknown. Symptoms were apparently paralysis of the hind-quarters and general weakening. To our knowledge only three were affected, and none died. No treatment attempted.' (H.J.)

Wabowden. '17 dogs were affected here with worms. They suffered from lassitude. Six died, and one was finally shot. Worm pills and other dog medicines were tried.' (G.L.R.L.)

+ *Pukatawagan.* 'Disease began in December, origin unknown. Dogs had diarrhoea and emaciation and some were paralysed in the hind-quarters. Most of the dogs here were affected and about 10% of these died. No treatment attempted.' (A.B.M.T.)

+ *South Indian Lake.* 'Disease began in December, with symptoms of distemper. 50% of dogs were affected and approximately 30–40% died. Distemper tablets were tried.' (W.J.H.)

+ *Nelson House.* 'Disease occurred in November, it came from rotten fish as food. Dogs got diarrhoea followed by cramps and usually died in several [days?] after first attack. About 70 dogs were affected throughout the winter, and about 50 died. No real attempt at treatment made—disease allowed generally to take its course.' (E.J.S.G.)

+ *Sand Lake.* 'Disease began in February. Symptoms were refusing food and discharging at the nose and mouth. All but one or two teams were affected and approximately 60% died. No treatment attempted.' (G.G.)

Saskatchewan

+ *Pelican Narrows.* 'Disease carried through from previous outfit, origin was fish liver flukes. Symptoms were lassitude, increasing debility, distended abdomen in later stages. 70–80% of dogs were affected and 70–80% died. Young animals mature on boiled fish but become infected after being fed raw fish for about three months.' (A.H.)

+ *Pine River.* 'Disease came from southern settlements approximately on April 15th. The dogs were very sluggish, no discharge from mouth or eyes. Severe attacks of diarrhoea, then they would run round as though mad, would wander off to die. Approximately 75% contracted it and of those infected about 30% died (i.e. 25 dogs). No treatment attempted.' (A.A.)

Clear Lake. 'Disease began in April, origin unknown. Symptoms were of distemper. About 10% of dogs were affected and four died. Treatment was attempted.' (P.P.)

Yukon

18. *Yukon Territory, south of Lat. 62°.* 'During the period mentioned, there have only been two known cases of sledge dogs dying of disease. These were isolated cases at points far separated. Both appeared to be distemper. One case occurred at Burwash Landing, Kluane Lake about February 1941, and the other occurred at Whitehorse, Y.T. on May 31st, 1941. The usual symptoms of distemper were in evidence in each case, and both dogs were destroyed. There had been no additional cases since then in either of the districts mentioned.' (B.A., Whitehorse.)

20. *Mayo.* 'Dogs subject to malnutrition and distemper all the year round. Disease confined almost entirely to Indian-owned dogs.' (J.S.)

Northwest Territories

1. MacKenzie River Valley

+ *Fort McPherson.* 'Disease occurred in February 1941, origin unknown. Symptoms were blood-flecked froth at mouth, squirming and scratching, stupor. About ten were affected and about ten died. No treatment was attempted.' (F.B.M.)

25. *Arctic Red River.* 'No epidemic. A few Indian dogs died of starvation.' (P.McK.)

8. *Point Separation.* 'Last [?year] three dogs died, in November. Symptoms were running nostrils and eyes and refuse food.' (E.L.)

2. Great Slave Lake Region

17. *Fort Smith.* 'A few dogs died of distemper last spring.' (H.A.McD.)

+ **27.** *Artillery Lake....* 'Disease occurred in April and May. The symptoms were loss of appetite, running at eyes and nose, pneumonia and finally convulsion and death. Two of my dogs had just loss of appetite and diarrhoea. One had loss of appetite, was unable to chew or swallow meat, died suddenly in convulsion. Two more had symptoms described above.' (A.J.K.)

Table 3 (*continued*)

+   **9.** *Reliance.* 'Disease, apparently distemper, with fits and dysentery, appeared in May. One of our dogs died on the trail back to home camp at Back River, having contracted disease at Reliance where all dogs were affected.' (M.P.M.)

3. Northern Coastline

+   **24.** *Krusenstern District.* 'Distemper acted in three different ways: (1) pains in back region, dying suddenly with severe pain. (2) dog sick: no pain, no sign, only dog weaker than usual. This continues until dog fades to skin and bone and usually dies slowly—some lasting three weeks. (3) Pus bag under head which I lanced: this dog is still alive. Dogs were dying all winter from October, last one died early in June. (L.F.S.)

+   **28.** *Coppermine.* 'Epidemic occurred December to March, symptoms: howling frequently night and day, mucus in eyes and nose, suffered much pain and tried to bite when I went near them. A dog standing up would suffer spasm of pain and collapse on ground howling. Lost four dogs and young pups. One dog was well at 2 p.m. and dead at 4 p.m. His death may have been caused from heart trouble.' (J.H.W.)

4. Large Islands

+   *Holman Island.* 'End of February, after arrival of Police Patrol from south. Some of their dogs were sick on arrival and one had to be shot second day after. Before that time there had been no sickness amongst dogs in this part of the district. Sickness quickly spread to other dogs and lasted right up till end of May. Symptoms were discharge from the nose and eyes, in quite a few instances nose and mouth, diarrhoea in varying degrees, fits and staggers. It was particularly noticed that dogs which had the diarrhoea in most cases recovered, and those that had fits etc. and no diarrhoea were the ones that died. It was also noticed that dogs which had been well kept and properly fed were in most cases immune but those that had a hard existence, died. Pups and dogs of about one year were the ones most susceptible. Degrees of mortality varied, some natives losing all their dogs, others just a few and in a couple of cases not at all, 40–50% would be a fair estimate.' (H.W.C.)

+   *Read Island.* 'Dog disease broke out at Coppermine early in the New Year (1941). The police patrol brought the first visiting dogs from the sick area and I asked them to tie their dogs out on the ice away from the local dogs; but it seems they did not do this at other places en route to Holman Island and return via Prince Albert Sound, so that actually the first dog sickness we had at Read Island was at Easter when dogs came in from the camps visited by the police. The mortality rate was high, but I do not believe it was so high as the epidemic of two years ago. The dogs that recovered from the sickness numbered about the same as the last sickness, but I have not heard of any dogs being blind on recovery as so often happened last time. I vaccinated my seven pups born in September 1940. One took the sickness shortly after they were vaccinated the first time. He was very sick with symptoms similar to distemper but only for a short time and he made a rapid and complete recovery. All seven pups have been raised successfully.' (F.R.R.)

+   **26.** *Cambridge Bay.* 'Outbreak occurred in January. Symptoms were loss of power in hind-quarters. Running eyes and nose. Continually passing green fluid. No appetite. 60% of dogs in locality died. Disease started at native camp. Malnutrition being underlying cause owing to lack of dog feed. Disease contagious and spread to healthy well-fed dogs. When no contact was made with diseased dogs there was no sickness.' (E.J.G.)

    Clyde River. 'No disease has been reported. Fair numbers of dogs died however from starvation and natives all say remnants of teams were much weakened due to lack of food.' (J.G.C.)

Hudson Bay and Inland

+   *Churchill.* 'Serious sickness, obviously distemper, began in January. 40% of the dogs were affected. Generally 25% but in some cases 50% [of those affected] died. Treatment was attempted as recommended, but very little success was achieved.' (A.B.U.)

    Nueltin Lake. 'A slight white eye discharge noted in March. No mortality or seeming lack of vigour.' (J.A.T.)

+   *Eskimo Point.* 'Disease began in March, by contact with teams from south which in turn contracted disease from Churchill dogs. Outbreak continued spasmodically until the end of May. Symptoms were running at the eyes, resulting in some cases in temporary blindness, general debility, and complete loss of appetite. In some cases dogs were affected with twitching of the eyes, ears and nose. Dogs affected by the disease seldom recovered. Inland natives lost 20%. Approximately two to three dogs out of every team of eight would be affected and about 20 dogs were affected locally; but disease was not considered as serious as north of Eskimo Point towards the vicinity of Tavane Post.' (W.C.B.)

+   **34.** *Eskimo Point* etc. 'Disease occurred about the first of the year and lasted from then to last of June 1941. Symptoms were signs of listlessness —discharge from the eyes and nose and loss of strength, also discharge of white foam from the mouth, sometimes paralysis of hind-quarters.' (H.O.H.)

+   **5.** *Eskimo Point to Padley.* 'Dogs were very badly affected. Symptoms were very different, but the one more common was blindness, running of the nose, diarrhoea (very badly) one week of life, sometimes less, and dead. Started in March, very bad in April and May. Another symptom of the disease was very strong colics (without diarrhoea), general shaking of all body, beating of the heart. Trying to vomit or cough. Sick for a week and death. The dogs in general have very bad tape worms in this district. Of course they eat meat most of the time. About one-third of the dogs die of the epidemic. About three-quarters had been sick. Eight-months pups more affected. Many females do not breed this spring.' (H.P.D.)

Table 3 (*continued*)

+   *Padley.* 'There is an epidemic among sledge dogs now (March 27th). This disease first appeared in here about three weeks ago when a dog team returned from Churchill. The sickness seems to be a mild form of distemper and a few dogs have died.' (D. D.)

+   *Tavane.* 'An epidemic, or, more properly two epidemics, broke out in the dogs at the end of March. Very few teams escaped. Sickness A was marked by loss of appetite and general debility at the onset. Later, the dogs afflicted suffered from acute ague and tottered about without apparently knowing what they were doing. This sickness seemed to be confined to the younger dogs and pups. It was, roughly, 25% fatal in the former and, at least, 50% fatal in pups. Sickness B was more of the usual distemper type and was marked with nose running and congestion of the lungs and chest. The mortality rate was not quite so high as in A and the sickness was more widespread, i.e. all dogs were subject to it. The indications are that B came from south via Churchill; but it is quite possible that A was contracted by dogs eating fox carcasses. It cannot definitely be said that there was an epidemic among the white foxes, but it is quite probable as it is definitely known that there was such an epidemic amongst wolves (which were very numerous during the winter). The possibility is that the disease was in the incubation phase in the foxes and was passed on to the dogs when they were fed the carcasses.' (G. A.)

+   *Chesterfield Inlet.* 'During April this disease was first observed around the Post, although reports from outlying camps were first heard in February. First reported after team had come in contact with dogs which had been to Churchill, Manitoba, where, we understand, the disease was very bad from December right on. Symptoms: refusing to eat, howling as if in great pain, slight pus around eyes and nose, unable to walk properly. Eventually lying down, and inside a week death would take place. A few cases were reported where the dogs just about heeled over in their tracks and died. In the observer's opinion, the pain which caused them to howl originated in the stomach and few, if any, got mad or ran around crazy as in previous epidemics. Mortality during the disease of this spring was practically 100%.' (J. L. F.)

+   35. *Chesterfield Inlet.* 'Disease occurred in May and June. It affected the dogs variously, but generally after a period of lassitude accompanied by a loss of appetite last[ing?] about two weeks a discharge of pus was seen from the nose and eyes. Some dogs had diarrhoea in the first stages. Some seemed to have a sort of twitching of the ears and eyelids. Some had convulsions. Most cases resulted in death. The disease was first reported south of here then it gradually worked along the coast to this point, the last reports were from *Cape Fullerton* where it is prevalent. Northward from that point it is not known whether the dogs are affected or not.' (L. C. E.) (2 +)

Table 4. *Observers' statements about lemmings (and 'mice') during* 1935–41

I. = increase, D. = decrease, N. = no change. s. = scarce, a. = abundant. (s. and a. are quoted only when a comparative estimate is lacking.) Heavy type means abundant. Observations on 'mice' (increase and abundance only) are given in brackets; most of these reports are by the same observers as for the lemming. Where there is more than one similar report this is shown 2, 3. Data are from Table 1 for each year. * shows that quotations from reports are given in the text or have been published elsewhere.

	1935–6	1936–7	1937–8	1938–9	1939–40	1940–1
Baker Lake	2D.	D.*	N.	2N.	2D. (I.)	I. D.
Adelaide Peninsula	2D.	*	N.	D.	I.	—
Perry River	—	I. I.	—	D.	—	I.
Kent Peninsula (and west)	—	—	2I.	—	D.	I.
Bathurst Inlet	I. (I.)* s.	2D.	N. (I.)	N. (I.)	—	I. N. (N.)
Beechey, Fry, Muskox Lakes	I.	I.	—	I.*	*	I.
Redrock, Providence, de Gras Lakes	s.	N.	N. I.	I.	N.	—
Mackay, Aylmer Lakes	N. I.	D.	—	D. N.	N.	—
Clinton Colden, Ptarmigan, Artillery Lakes	I.	2I. D.*	I.	D.	3N.	I. N.*
Headwaters Thelon River	I. N. s.	2I. D.*	—	—	D.	
Coppermine east to Kugaryuak, west to Stapylton Bay	I. I. 2D.*	3N.	2N.	2D. (I.)	I. (I.)*	3I. a.*
Dismal Lakes, Great Bear Lake	—	—	I. I.	N. (I. I.)	N.	
Pearce Point to Richards Island except Baillie Island	N.	I.	D.	2D. (I.)	—	D. (I.)
Baillie Island	I. D.	I.*	I.	D.	N.	2D.
Mackenzie River delta	D.	D.	2I. D.	N.	D.	I. a. (I.)
West of delta	D.	D.	N.	—	—	—

REVIEWS

THE JOURNAL OF ECOLOGY
(Vol. 30, No. 2, August 1942)

THIS number contains 153 pages and includes five original papers, two reviews and a contribution to the Biological Flora of the British Isles.

The original papers all deal with various aspects of freshwater ecology. In the first of these J. W. G. Lund describes work on the marginal algae of certain ponds in Richmond Park. Stability and seasonal changes in the organic matter of the underlying muds are shown to be important in controlling the algal communities. S. P. Chu describes methods which have proved successful in the pure culture of fresh-water planktonic algae and gives the evidence obtained as to the nutritional requirements of certain of these algae. Winifred Pennington gives data for the utilization of nitrogen by fresh-water algae and records nitrogen losses under certain conditions. In a paper on the algae of Miles Rough Bog near Bradford, Yorkshire, A. Malins Smith summarizes the results of five years work and discusses the results in the light of observed secular changes and the nature of the water supply. A very detailed analysis of the conditions controlling the oxygen concentrations in a small Welsh pond and its inflowing stream is contributed by E. M. O. Laurie. The results are contrasted with similar information about waters richer in mineral salts.

A number of the Biological Flora is included dealing with *Aster tripolium* L. It is compiled mainly from the data of V. J. Chapman, by A. R. Clapham, W. H. Pearsall and P. W. Richards. The reviews deal with the *Journal of Animal Ecology* and with a book on Ecological Crop Geography by K. H. W. Klages.

<div style="text-align: right">W. H. PEARSALL</div>

BIOLOGICAL FLORA OF THE BRITISH ISLES

A proposal for a British 'Biological' Flora was first put forward by Prof. E. J. Salisbury in 1928. In January 1940, the Council of the British Ecological Society decided to take up this project and arrangements have now been made for publication. The first seven parts have already appeared in the *Journal of Ecology*: on some rushes of the genus *Juncus* (vol. 29: 362–91), the sedge *Cladium mariscus* and the eel-grasses *Zostera marina* and *hornemanniana* (vol. 30: 211–16, 217–26). The Council have constituted an Editorial Committee consisting of the Honorary Editor of the *Journal of Ecology* (Prof. W. H. Pearsall), Dr A. R. Clapham and Dr P. W. Richards.

The Flora will consist of accounts of single species or small groups of species and will appear part by part as material becomes available. A list of projected parts (twenty more species) is given (*J. Ecol.* 29: 361). It is, perhaps, a reflexion on orthodox taxonomy that there should be felt to be much difference between a 'Flora' and 'Biological Flora'. What is meant by the latter term is shown in the schedule for prospective authors (*loc. cit.* pp. 358–60). It is hoped to include information, as far as it is available, under ten main headings. *First*, the general distribution of the species will be outlined, with altitudinal limits. *Second*, all that is known of the habitat in which the species lives. *Third*, the plant communities in which the species is found and the other species which associate most closely with it. *Fourth* and *fifth*, the response of the plant to biotic factors, such as competition with other plants and the effect of grazing by animals. This is a subject to which animal ecologists could make a great contribution. Not nearly enough is known about which plants different species of animals graze, what plants they prefer when a choice is available, and how plants stand up to grazing by different animals. *Sixth*, the functional morphology of the plant, e.g. root-system, mode of perennation, age at first flowering. *Seventh*, phenological data, particularly times of maximum vegetative growth, of flowering and of seed-setting. *Eighth*, methods of reproduction. There are two questions here in which animal ecologists are concerned and about which much more information is required. The first is the list of insects or other animals which pollinate the flowers. The data are very incomplete and relatively little has been published in this country. There is almost no information about insect visitors in different parts of the country or in different habitats. The second point is the role of animals in the dispersal of seeds. While there are some records of birds feeding on

berries of the best-known plants, such as hawthorn or yew, little is yet recorded of feeders on such plants as buckthorn, for instance, which is nevertheless not a rare plant.

The *ninth* main heading deals with plant parasites, whether animal or vegetable. The most important are the phytophagous insects and the Fungi. A complete list of the insects feeding on some of our commoner plants would be extremely long and, in view of the many general feeders, difficult to make complete. It is intended therefore only to list species which are restricted to one or a few genera of food plants. General feeders will only be mentioned when they are known to affect plants seriously. Finally, under the *tenth* heading, information will be given about the past history of the species in the British Isles. In all the larger plant genera there will be an introduction to the whole genus. The parts will be issued separately at 1*s.* or a standing order may be placed (at the Cambridge University Press) for all parts at 9*d.* each.

Animal ecologists will find in this work a great deal of useful information which it is very difficult for them to get elsewhere.   O. W. RICHARDS

THE NORTHERN ECOLOGICAL ASSOCIATION

Although there is still a vast field of enterprise for the individual naturalist, working alone for his private pleasure, or as an expert on some particular group of plants or animals, there has lately been need for a little organization, to give coherence and shape to local surveys, and to provide opportunities for the many people who, though not trained ecologists, yet enjoy participating in field work which they know will be of general interest and value, and which will build up gradually some dynamic picture of the wild life of the country they live in. The Northern Ecological Association was founded by the late Mr R. J. Flintoff and a small group of naturalists connected with the *North Western Naturalist*, an excellent regional natural history journal, whose papers have frequently been abstracted in the *Journal of Animal Ecology*. In 1941, the Association was given a more formal shape and organization. Its announced aims include the following admirable targets for research: 'The intensive study of small areas, year after year, in as many branches of natural history as possible, in order to learn the relation of living things to their environment, and to one another, and the history of a single species.' 'History' is here, presumably, used in the old sense in which it meant an account of the species, whether from a historical standpoint or not, this being the original meaning of 'natural history'. Members already number several hundred, and they are enjoined to band together into district groups, and organize surveys of specially suitable areas, and to aim at producing work of an order high enough to be published in regional natural journals, or in those of the learned societies. 'We attach no importance to the long lists of living things, with little or no data, appearing in the journals.... We hold no meetings and take no excursions, because we believe that however pleasant and amusing such entertainments may be from a "hiking" or social point of view yet they do little or nothing to advance the serious study of field natural history.' It was time somebody said this! But the organizers of the surveys will still have to watch keenly in order to prevent a relapse into the comparatively lazy and butterfly-like habits of most field excursions in parties. Even in the British Ecological Society, which stands for a sympathetic understanding of wild plant and animal life, I have attended a summer meeting at which a phalanx of members marched unpityingly through the woods, tramping flat a lane several feet wide, and leaving for the animal ecologists only the study of the blood-sucking flies attracted by an unusual abundance of human food. The Northern Ecological Association has wisely placed emphasis on the steady investigation of small local areas. The first of these to be studied was the Hole of Horcum, a basin in the hills of the North Riding. More recently the moorland district of Goathland has been investigated, and an interesting report on the habitat distribution of the birds (W. S. Medlicott (1940), *Northw. Nat.* 15: 28–40, 109–26) published. Other notes and papers on these areas have appeared in the same journal, and some have been abstracted in the *Journal of Animal Ecology* from time to time.

These surveys follow much the same general lines of others organized by Universities or natural history societies, e.g. of Wicken Fen by Cambridge University, of Rostherne Mere by Coward and other earlier Cheshire naturalists, of Limpsfield Common by the London Natural History Society. The treatment is primarily by taxonomic groups, usually of those which are in a state to be treated at all by amateur or local workers. The surveys cannot be complete, partly because of the limitations of time and observation, but also because a number of invertebrate groups are still taxonomically difficult and will in some instances always remain the preserve of the highly experienced specialist. Even allowing for all these difficulties, which are well known to (one almost said, branded in the minds of) those who attempt to make an organized study of animal communities by means of field surveys, one misses any solid attempt to pull

the different parts of the surveys into coherent shape. One is left with the mpression that the animals are still being treated as if each taxonomic group was living a separate life, uninfluenced by the presence of others. Or perhaps it would be fairer to say, that it is to be hoped that the necessary preliminary stage of lists and group surveys will be followed by thoughtful discussions of the relations between the different species, which should in turn lead to a host of fruitful special field problems of the kind that the naturalist should be especially interested to solve. If the Northern Ecological Association succeeds in doing this, it will have broken entirely new ground in British local natural history, and shown that the naturalist deserves to have a good deal of say in the planning and control of regional recreational areas and nature reserves—subjects which will at once spring into importance when post-war national planning is being built up.

The present Secretary of the Association is Mr J. L. Forrest, Eversfield, Goatland, York. For a small subscription, naturalists can belong to the Association and also receive the *North Western Naturalist.*

<div align="right">CHARLES ELTON</div>

A GUIDE-BOOK TO TAXONOMIC LITERATURE

John Smart (1942). (Editor.) *Bibliography of key works for the identification of the British Fauna and Flora.* Association for the Study of Systematics in Relation to General Biology, Publication No. 1, 105 pp. On sale at the Linnaean Society, Burlington House, Piccadilly, London, W. 1, and Messrs Adlard and Son, Ltd., Bartholomew Press, Dorking, Surrey. Price 7*s.* 6*d.* (post free).

Although little has been seen in print on the subject, yet there has been a great deal of private discussion of the relation between systematists and ecologists not without a good deal of criticism on both sides. Systematists cannot see why anyone should want to make what seems to them a superficial study of all the animal groups that live in one habitat or locality, or if they are sympathetic with the ideal of ecologists they still feel that the ecologist must learn to identify species himself and not keep sending in enormous consignments of material to museums for the specialist to name. The systematist is often like a skilful builder, who puts a great deal of trouble and care into the erection of a building, but when it is finished may take little interest in what goes on inside it, who lives in it, what use is made of it. The fun for him is in describing and relating his description to other mosaics of species. He feels towards the survey ecologist rather as a builder would if telegraph messengers kept running up to him in the middle of another big job, asking him the name of that building near St Paul's Cathedral, which turns out after all to be only the General Post Office, and which anyone should have known by sight, even if he is a native of Amsterdam who has never been in London at all, and wants to find out something about the interrelations of London life. On the other hand, community surveys, community distribution and structure, and the mass population dynamics of communities, necessitate large collections of animals—larger than any specialist wants to name and larger than any museum wants to house—and some method must be arrived at for ensuring that they are correctly named, and that some proportion of the material is stored as 'vouchers' for the work in future years, when the taxonomic definitions may have changed, or new species splits (real or artificial) have been decided on. In the parable given above, the real answer to the stranger's difficulty would be to ask the way of a policeman, whose job it is to name buildings and provide guides through the maze of London's streets and alleys. The same answer will have to be given to the ecologist, sooner or later, and museums will undoubtedly have to provide a greater service for straightforward identification, as distinct from the highly specialized and equally important research on new species and new classifications, which is the normal job of trained taxonomists at present. Such service, is, in fact provided for the British Empire, through the Imperial Institute of Entomology, using the resources of the British Museum of Natural History, and there seems no reason why an equally good one should not be built up for the use of British ecologists working in their own country. Indeed, there is much more likelihood of fundamental discoveries in synecology being made by British workers, than by those who are necessarily engaged on a great deal of applied ecology of a short-term nature. With the growth of national parks, nature reserves, and biological education, there will be a great increase in interest in our ecological problems, and the development of scientific farming and of scientific pest control generally will create similar demands for a properly based Ecological Survey.

Let us not deny that many ecologists could give closer attention to the identification of their own specimens, and it is well known that many are willing to do so provided they can be assured that their work will be based on reliable books and that they will be told when they ought to seek more specialized advice. What cannot be tolerated is any suggestion that because community surveys are extremely difficult and laborious to do and are a potential nuisance to systematists, they should be laid on the shelf. One's impression is that this matter is much better organized in the United States than it is in this country, perhaps because a great deal more money and enterprise have been poured into the development of museum services.

The Association with the trinomial name (which might well be a little shortened for reference) has done an excellent task in promoting the publication of this useful guide. Most ecologists have been praying for text-books and check lists on every group, and a guide to the literature. We are still far short of a complete set of works for identification, and many of those that exist are ill-suited to the ecologist's purpose. Thus there is no simple book on British molluscs, no complete text-book on the identification of British spiders, and no modern work on British reptiles and Amphibia. At the same time there has been an impressive advance in the clearing-up of certain groups, such as the blood-sucking flies, the fresh-water Copepoda, and in bringing up to date knowledge of British birds. In this sphere the Ray Society has done consistently good work, with its beautifully produced monographs, and also the various entomological and ornithological societies.

The Bibliography gives a pretty complete panorama of the main authoritative works on each group, both of animals and plants, and some brief but valuable indications of their scope and reliability. One notices a certain number of omissions, which are no doubt due to differences of opinion among taxonomists. Two rather odd omissions are Macan's keys to Corixidae and to Water Bugs, published as Nos. 1 and 4 of the excellent series from the Freshwater Biological Association at Windermere. Sandars's butterfly book for the pocket is also omitted: although having no pretensions to originality of content, it has charm and simplicity of expression, and happens to be available when Frohawk's larger book is out of print. These are small points, however, and can be easily considered for future editions, of which one hopes there will be many. One important correction should be included: the *Notices of Publications on the Animal Ecology of the British Isles*, which are mentioned in the remarks on 'Current Literature', are published in this *Journal*, not the *Journal of Ecology*, although they originally began in the latter in 1928.

Ecologists who use this authoritative guide should bear in mind that it does not usually warn him about the possible snags in identifying particular groups of species, and it is in no way an all-clear sign for him to ignore taxonomic difficulties. It simply tells him what has been published, with a bare mention of the scope of each work. It will be a sound working rule, until the ecologist has mastered thoroughly the systematics of a particular group, to make his identifications provisionally himself, so far as is physically possible, but to get samples confirmed by authority before final publication. It is a rule of the *Journal of Animal Ecology* that survey papers are only accepted on the understanding that sample specimens will also be deposited in some institution for reference.

The field ecologist now has some magnificent publications to use. With A. G. Tansley's *The vegetation of the British Islands* (1939) to give a thorough background of physical and vegetation conditions, it ought to be possible to develop after the War a wider knowledge of animal communities, and eventually to build up a fairly complete Ecological Survey for animals. CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the paper to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W.1, or through a bookseller, price 3s. 6d. per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, R. B. Freeman, B. M. Hobby, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(a) Marine and brackish

Bassindale, R. (1942). 'Studies on the biology of the Bristol Channel. VIII. An account of collecting stations, and corrections to the fauna list.' Proc. Bristol Nat. Soc. 9: 304–15.

A general description with map of the collecting stations that have been used for other studies in this series of papers. Stations are described from Haw Bridge below Tewkesbury to Ilfracombe.

Lloyd, A. J. (1942). 'Studies on the biology of the Bristol Channel. IX. A survey of the fishing industry at Weston-super-Mare during the winter of 1940–41.' Proc. Bristol Nat. Soc. 9: 316–27.

Chiefly deals with the old-established sprat fishery which is commercially important from November to February. Notes on fishing technique and size variation of sprat and whiting are given.

Matthews, L. H. (**1942**). 'Studies on the biology of the Bristol Channel. X. The catches of a Somerset fish weir.' Proc. Bristol Nat. Soc. 9: 328–34.

Fish weirs or hangs are V-shaped fences with the apex pointed seaward which catch fish on the ebb tide. The present one was made of wire-netting fastened to stakes. The principle catch was small flat fish with seasonal appearance of whiting, codling, and other species. The size of catch is correlated with wind direction; in general the best catches were made when the wind was in the least frequent quarters. The catch fell off year by year until the weir was abandoned. It is suggested that inshore fish have a very limited movement range and a fixed net quickly fishes out the marketable fish.

Bassindale, R. (**1942**). 'The distribution of Amphipods in the Severn Estuary and Bristol Channel.' J. Anim. Ecol. 11: 131–44.

This paper is No. 7 of a series on the biology of the Bristol Channel and deals with the commonest species of Amphipods found between low and high tide levels from Blue Anchor in the Channel, with a salinity of around 30 g.p.l., to Tewkesbury in permanently fresh water. Most attention is paid to *Gammarus* and *Marinogamarus*. Changes in distribution between spring and summer are not outstanding. After the severe winter of 1939–40 three species showed intersexes and inhibited breeding in females in the less saline end of their range. A comparison of the distribution of the species of these two genera in the Severn with that in other estuaries agrees with salinity requirements, with some exceptions, notably in the Tay.

Powell, D. F. W. Baden– (**1942**). 'On the marine Mollusca of Studland Bay, Dorset, and the supply of lime to the sand dunes.' J. Anim. Ecol. 11: 82–95.

The rate of change in the plant and animal environment here is known because sand dunes have accumulated from the seventeenth century. The lack of lime is considered to be due to lack of shell fragments, which is not due to lack of marine Mollusca, but to absence of grinding action by strong waves owing to the sheltered position of Studland Bay. Shells of 56 species were identified and are listed.

Hornell, J. (**1942**). 'The importance of the lug-worm in the cleansing of littoral sands.' Hastings Nat. 6: 90–3.

Arenicola sp.

(*b*) FRESH WATER

Mortimer, C. H. (**1942**). 'The exchange of dissolved substances between mud and water in lakes.' J. Ecol. 30: 147–201.

This very detailed study (continued from *J. Ecol.* (1941) 29: 280–329) of the physico-chemical processes occurring in the bottom mud and overlying water of lakes is of interest to animal and plant ecologists because the results of the processes affect the productivity of lakes. Reduction of the oxygen in the mud surface is associated with increase in the supply of solutes to the water which may be expected to augment plankton production.

Macan, T. T., Mortimer, C. H. & Worthington, E. B. (**1942**). 'The production of freshwater fish for food.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. No. 6: 1–36.

This is a practical guide to fish farming, with selected references. Ponds or waste swampy land might be expected to yield fish crops comparable with the weight of meat produced on some pasture lands. Methods of increasing the fertility of fishponds include the use of artificial fertilizers. Research is needed into the practicability of sewage fishponds. Far greater exploitation of silver eels should be carried out.

Worthington, E. B. (**1942**). 'Perch trapping.' Salm. Trout Mag. Lond. No. 104: 64–8.

A description of the methods and gear used to trap perch at spawning time.

Marshall, J. F. & Attwooll, A. W. (**1941**). 'The mosquito-breeding possibilities of static water supplies.' Mimeographed leaflet, 7 pp. and 1 Plate, issued by The Limmer and Trinidad Lake Asphalt Co. Ltd., 19 Grosvenor Place, London, S.W.1.

Discussion of the effect on mosquito populations of increased static water supplies for fire-fighting. It is concluded that only three species are likely to be important: *Culex pipiens*, very common but practically never biting man, only birds, etc.; *Theobaldia annulata*, mainly confined to water polluted with nitrogenous matter like sewage, though fierce biter of man, with serious reactions; and *Culex modestus*, probably occurring mainly in underground tanks, not open ones on surface, bites man, but can breed without a blood meal. Practical policies arising from these facts are discussed. Treatment of the water need not be done until a survey has proved the presence of a dangerous species. Oiling the water surface causes deterioration in asphalt or bituminous linings of tanks.

Marshall, J. F. (**1942**). 'Mosquito-breeding in static water supplies.' Nature, Lond. 149: 568.

Covers the same ground as the pamphlet by **Marshall and Attwooll** (**1941**).

Popham, E. J. (1942). 'The influence of light in the migration of Corixidae.' Entomologist, 75: 77–80.

Sigara distincta does not orientate itself to light when submerged; wet insects turn away from light, possibly to facilitate the drying of the wings; dry insects face the light before flying, the initial direction of flight is towards the sun and then later towards any bright object.

Reynoldson, T. B. (1942). '*Vorticella* as an indicator organism for activated sludge.' Nature, Lond. 149: 608–9.

The density of ciliates, *Vorticella* spp., showed a high degree of negative correlation with oxygen absorption and biological oxygen demand of sewage sludge. Quantitative determinations can be made very quickly and offer a good method of telling the condition of the activated sludge.

Barker, A. N. (1942). 'The seasonal incidence, occurrence and distribution of Protozoa in the bacteria bed process of sewage disposal.' Ann. Appl. Biol. 29: 23–33.

The fauna was studied through a year and compared with that of the Imhoff digestion tanks and of the activated sludge process. Fluctuations of the fauna of the sedimentation tanks appear to be dominated by sporadic change in the character of the sewage, but in the bed and humus tanks seasonal variations occur in all forms, especially in the Ciliata, changes in abundance occur in the peritrichous forms, and in other ciliates a seasonal succession of species is noted.

(c) Land

Pickles, W. (1942). 'Animal mortality on three miles of Yorkshire roads.' J. Anim. Ecol. 11: 37–43.

Invertebrates comprised 87·3% of the total numbers, Hymenoptera representing 49·5%, chiefly bees. Among the vertebrates, mammals constituted 2·9%, birds 7·3% and amphibians 3·5% of the total for all animals, which was 687, or 229 per mile, for the year. The highest mortality was in August. The dead insects are a source of food for ants.

Ruck, A. (1941). 'Camouflage.' J. Soc. Pres. Fauna Emp. Part 44: 14–9.

General essay with four photographs.

Rothschild, M. (1942). 'Change of pelage in the stoat *Mustela erminea* L.' Nature, Lond. 149: 78.

Several observations on captive stoats. The autumn moult occurs in late November and may be completed in from 20 hours to 20 days, depending on temperature. The spring moult in February may last for several weeks.

Lloyd, B. (1942). 'A new Hertfordshire mammal: Natterer's Bat.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 21: 316.

Record from an elm tree hole in 1898.

Colquhoun, M. K. (1941). 'Visual and auditory conspicuousness in a woodland bird community: a quantitative analysis.' Proc. Zool. Soc. Lond. A, 110: 129–48.

A coefficient of conspicuousness (total birds/birds seen during an hour's walk) is worked out for all species. It varies from 0·22 (chiff-chaff) to 0·86 (hedge sparrow). Records were also taken of the abundance of species in the different strata, the mistle thrush appearing most often in the canopy, and the hedge sparrow on the ground. Seasonal and sexual variation in conspicuousness are also dealt with.

Harrison, J. G. (1941). 'Handbook of birds of the Malvern District.' 56 pp. (half left blank for notes), 1 pl. Univ. Lond. Press Ltd., St Hugh's School, Bickley, Kent. Price 2s. 6d.

The area covered lies mostly to the east of Great Malvern and extends to Leigh, Worcester, Evesham, Tewkesbury. Part of the Severn is contained in this area, and there are two parks, a sewage farm, a lake and much common land. 144 species have been recorded, of which 34 are only occasional visitors. Interesting notes on change of status in various species since 1886 are given.

Arnold, E. C. (1940). 'Bird reserves.' 216 pp., 21 illust. H. F. & G. Witherby and Co., London. Price 15s.

A general account of birds and flowers, but chiefly the former, in the neighbourhood of Eastbourne with some notes from Norfolk. A few hints are given on establishing cover round an old pond, planting of water lilies, willows, etc. A note says that driving in a stake beside new saplings will prevent damage by *Apodemus*.

Fitter, R. S. R. (1941). 'Report on the effect of the severe winter of 1939–40 on bird-life in the area within 20 miles of London.' Brit. Birds, 35: 33–6.

Not many cases of actual deaths are reported, but numbers of birds were very tame and changed their feeding habits to the extent of coming into gardens. Big movements of skylarks and fieldfares were noted. Decreases in subsequent breeding populations were noted in reed buntings, stonechats, house-sparrows, creepers, wrens and herons.

Kloet, G. S. (1942). 'Improvements to Burke's trap for wood-boring insects.' Ent. Mon. Mag. 78: 61–3.

This is a small cage which can be attached to logs, etc. It is equipped with a glass tube in which the insects collect on emergence.

Niblett, M. (1941). 'Some Diptera inhabiting thistles.' Northw. Nat. 16: 278 81.
Notes on Trypetids and Cecidomyids.

Pickles, W. (1942). 'Mound building by the ant *Lasius flavus* F.' Ent. Mon. Mag. 78: 38–9.

In 8 weeks during which three nests of this ant were under observation 404·3 g. of soil was used as building material = 134·8 g. per nest.

Butler, G. C. & Finney, D. J. (1942). 'The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and solar radiation.' J. Exp. Biol. 18: 206–12.

Variations in bee activity were associated with the radiation of clear light, not of ultra-violet as claimed by previous workers.

Lloyd, B. (1942). 'The hornet in Hertfordshire.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 21: 304–7.

Record of a nest at Berkhamstead in 1940. Records for this county are few.

Jarvis, F. V. L. (1941). 'The nature of hibernation in Lepidoptera.' Proc. S. Lond. Ent. Nat. Hist. Soc. 1941—42: 1–10.

Notes on hibernation in a number of species. A biochemical inhibitor is postulated to account for the condition found in true hibernators, species whose cycle cannot be accelerated by heat.

Gunn, D. L. & Hopf, H. S. (1942). 'The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. II. The amount of locomotory activity in relation to experimental and to previous temperatures.' J. Exp. Biol. 18: 278–89.

The proportion of these spider-beetles walking about at random instants was observed in dishes immersed in water baths at constant and changing temperatures. Activity depended on the temperature at which the culture had been reared: e.g. those previously kept at 28° C. were always more active than those previously kept at 16° C. when both were exposed to the same conditions. Temperatures rising or falling fast had a pronounced stimulation on activity: e.g. at 20° C. 90 % became active as a result of these changes while at constant temperature only 25 % were moving.

Ewer, D. W. & Ewer, R. F. (1942). 'The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. III. The effect of temperature and humidity on oviposition, feeding and duration of life cycle.' J. Exp. Biol. 18: 290–305.

At 70 % R.H. *P. tectus* completes its development in the shortest time at the surprisingly low temperature of 23–5° C. Favourable humidities are of the greatest importance in the life cycle. With low humidity hatching may not occur despite full embryonic development, and at high temperatures hatching will not occur except in 100 % R.H. Below 70 % R.H. feeding is much reduced in the absence of drinking water.

Grant, F. T. (1942). 'Coleoptera taken on and in a garden refuse heap.' Ent. Rec. 54: 63.
A list of 22 species from Gravesend.

Grant, F. T. (1942). 'Coleoptera in stack refuse.' Ent. Rec. 54: 64.
58 species were taken in one haystack near Gravesend, December 1941.

Coe, R. L. (**1942**). '*Rhingia campestris* Meigen (Dipt., Syrphidae): an account of its life-history and descriptions of the early stages.' Ent. Mon. Mag. 78: 121–30.

The larva of this common hover-fly breeds in cow-dung.

Proceedings of the Association of Applied Biologists (**1942**). 'Symposium on wire-worm investigations.' Ann. Appl. Biol. 29: 144–96.

Includes introduction by **J. C. F. Fryer**, wireworms and crop production by **S. G. Jary**, statistical problems in field sampling by **F. Yates** and **D. J. Finney**, some factors influencing growth in *Agriotes* by **A. C. Evans** and **H. C. Gough** and observations on the biology of the adult *Agriotes obscurus* by **M. Cohen**.

Reid, J. A. (**1942**). 'A note on *Leptinus testaceus* Müller (Coleoptera: Leptinidae).' Proc. R. Ent. Soc. Lond. A, 17: 35–7.

This blind beetle occurs in nests of *Apodemus sylvaticus*. The head and mouth-parts of the larva are described. The possibility of three generations a year with peak emergences of adults in May, September and December, is suggested.

Sargent, H. J. (**1942**). 'On the occurrence of *Atypus affinis*, Eich. in East Sussex.' Hastings Nat. 6: 83–6.

The only British species of the Mygalomorphae spins purse webs on friable banks. It is confined to the south of England. Sussex records are given.

Heeley, W. (**1941**). 'Observations on the life-histories of some terrestrial Isopods.' Proc. Zool. Soc. Lond. B, 111: 79–149.

A very full account of the species *Trichoniscus pusillus, Porcellio dilatatus, P. scaber, Oniscus asellus, Philoscia muscorum, Armadillidium vulgare*. Notes on habitat and collecting are given, and the importance of humidity in determining distribution stressed. The main part deals with the life-history of each species.

Collinge, W. E. (**1941**). '*Porcelionides cingendus* Kinahan, a woodlouse new to Wales.' Northw. Nat. 16: 326–7.

This species, known from Spain, France, Cornwall and Ireland, is recorded from the Mumbles, Swansea.

Collinge, W. E. (**1941**). 'Notes on the terrestrial Isopoda (woodlice). No. I.' Northw. Nat. 16: 122–7.

Observations were made on colonies of *Platyarthrus hoffmannseggii*, the blind woodlouse, kept in flat glass dishes. Pairing took place in April and incubation was 20–30 days, broods of fifteen to twenty young being produced. There was usually a second brood. Literature on regeneration in woodlice is reviewed and some further observations included.

Collinge, W. E. (**1941**). 'Notes on the terrestrial Isopoda (woodlice). No. II.' Northw. Nat. 16: 247–56.

Notes on hibernation and reproductive habits in various species. A method is given of distinguishing the genera of British woodlice on the characteristics of the telson and urapods.

Carrick, R. (**1942**). 'The grey field slug *Agriolimax agrestis* L., and its environment.' Ann. Appl. Biol. 29: 43–55.

The physical environment as studied in the laboratory and correlated with conditions in the field. This slug tolerates a wide range of soil pH. The densest populations are in soils of high water-holding capacity. The ranges of temperatures for the survival, oviposition and hatching of the slug are given. Normal extremes of weather in Britain are not usually lethal but they do inhibit adult activity and reproduction.

Barnes, H. F. & Weil, J. W. (**1942**). 'Baiting slugs, using metaldehyde mixed with various substances.' Ann. Appl. Biol. 29: 56–68.

Incidentally indicates the catholic taste of the species of slugs occurring in gardens and effect of rain on their activity.

Miles, H. W. & Miles, M. (**1942**). 'Investigations on potato root eelworm, *Heterodera rostochiensis* Wollenweber. On the cyst population of a field over a series of years.' Ann. Appl. Biol. 29: 109–14.

The period of 7 years between the potato crops of 1928 and 1936 was not long enough for all cysts to lose their viability, although all signs of 'potato sickness' disappeared.

(*d*) Small islands

Lack, D. (1942). 'Ecological features of the bird faunas of British small islands.' J. Anim. Ecol. 11: 9–36.

The smaller and more remote the island the less the number of breeding inland bird species compared with the mainland. This is partly due to habitat limitations, partly to small size of population and consequent liability to extinction and partly to the sea, which temporarily checks the species which are spreading. Distributions among islands are often erratic, populations are represented by small numbers, and there are marked changes in abundance. Many fluctuations are due to mortality factors not dependent on density. Marked habitat changes have been recorded for seven species. The foregoing applies to a less extent to sea and shore birds.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF
USE TO ECOLOGISTS

Ellerman, J. R. (1940). 'The families and genera of living rodents. With a list of named forms (1758–1936) by **R. W. Hayman** and **G. W. C. Holt**. Vol. I. Rodents other than Muridae.' 689 pp.; and text-figures. (1941). Ibid. 'Vol. II. Family Muridae.' 690 pp.; and text-figures.

A valuable source for taxonomy and nomenclature of rodents. Essential for reference.

Tetley, H. (1941). 'On the Scottish wild cat.' Proc. Zool. Soc. Lond. B, 111: 13–23.

Examination of a number of specimens from Perthshire indicates that the Scottish race is not so markedly separated from the Continental as has been thought. Measurements show similarity to the south Spanish race (*Felis silvestris tartessia*). Tooth wear is an unreliable indication of age and the condition of the epiphyses is a better criterion.

Tetley, H. (1941). 'On the Scottish fox.' Proc. Zool. Soc. Lond. B, 111: 25–35.

Specimens from Perthshire confirm that mountain foxes are greyer than lowland ones, but suggest that they are smaller in size instead of larger, as previous authorities have said. Data on the growth of the cubs. A comparison with Continental material confirms the distinctness of the mountain subspecies. Scandinavian foxes also belong to this type.

Witherby, H. F. (1941). 'A check-list of British birds, with a short account of the status of each (Revised Edition).' 78 pp. H. F. & G. Witherby Ltd., 326 High Holborn, London, W.C.1. Price 5*s*.

Lists 520 species of birds: 147 resident species or subspecies, breeding regularly; 52 summer visitors; 82 regular winter visitors and passage migrants; 238 occasional and irregular visitors; and one—the great auk—extinct.

Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1940). 'The handbook of British birds. Vol. 4 (Cormorants to crane).' Pp. 1–461. (1941). Ibid. 'Vol. 5 (Terns to game-birds; additions and corrections; systematic list and indices).' Pp. 1–356. Both volumes fully illustrated in colour and with text-figures. H. F. & G. Witherby, Ltd., 326 High Holborn, W.C.1. Price £1. 1*s*. per vol. for subscribers to all five volumes; £1. 5*s*. for single volumes.

These volumes complete an authoritative work that contains much summarized information on ecology, though without many literature references.

Bullough, W. S. (1942). 'On the external morphology of the British and Continental races of the starling (*Sturnus vulgaris* Linnaeus).' Ibis, 6: 225–39.

A full description is given of the plumage differences between British and Continental starlings. These are actually slight and the main difference is physiological in the time of assumption of breeding plumage, which is much earlier in British birds.

Kloet, G. S. (1942). 'An improved breeding cage.' Ent. Mon. Mag. 78: 58–60.

This cage is provided with glass tubes in which insects collect on emergence.

Audcent, H. (1942). 'Hints on the mounting of Diptera.' Ent. Rec. 54: 69–72.

Van Emden, F. (1942). 'The collection and study of beetle larvae.' Ent. Mon. Mag. 78: 73–9.

Describes and figures a convenient method of storing and labelling large numbers of spirit specimens.

Van Emden, F. I. (1942). 'A key to the genera of larval Carabidae (Col.).' Trans. R Ent. Soc. Lond. 92: 1–99.

A very important paper illustrated with 100 text-figures.

Reid, J. A. (1942). 'The species of *Laemophloeus* (Coleoptera: Cucujidae) occurring in stored foods in the British Isles.' Proc. R. Ent. Soc. Lond. A, 17: 27–33.

Gives key for identification of five species.

Beirne, B. P. (1942). 'The morphology of the female genitalia of the Lepidoptera.' Ent. Rec. 54: 81–3.

Beirne, B. P. (1942). 'The morphology of the male genitalia of the Lepidoptera.' Ent. Rec. 54: 17–22, 37–9.

A very useful account of the homologies and terminology of these organs.

Hickin, N. E. (1942). 'Larvae of the British Trichoptera.' [1–4.] Proc. R. Ent. Soc. Lond. A, 17: 9–11 [12–13, 14–16, 16–17].

Describes larva and habitat of *Stenophyllax stellatus, Triaenodes bicolor, Rhyacophila dorsalis* and *Philopotamus montanus.*

Scourfield, D. J. (1942). 'The "*Pulex*" forms of *Daphnia* and their separation into two distinct series, represented by *D. pulex* (De Geer) and *D. obtusa* Kurz.' Ann. Mag. Nat. Hist. 9: 202–19.

Many forms have recently been reunited under the specific name *D. pulex* since their characters, being very variable, have no specific validity. It is shown here that a series of eight defined characters separate *D. pulex* from *D. obtusa*. The most obvious of these is the presence in the latter only of a row of long, plumose setae on the inner lip of the ventral margin of the valves. It is suggested therefore that these two forms at least should be regarded as separate species.

Lowndes, A. G. (1942). 'Rapid determination of water in animals and plants.' Nature, Lond. 149: 79.

Distilling the tissue in xylol or toluene may perhaps remove the bound water which is not removed *in vacuo* or in oven drying.

3. PARASITES

Morison, G. D. (1942). 'Sheep strike by the fly, *Phormia terrae-novae* R.-D., in north-east Scotland.' Nature, Lond. 149: 358.

P. terrae-novae is abundant in north-east Scotland, but this is the first record of it attacking sheep. Its habits and life-history are little known; the usual species causing strike is *Lucilia sericata*.

Williams, D. W. (1942). 'Studies on the biology of the larva of the nematode lungworm, *Muellerius capillaris*, in molluscs.' J. Anim. Ecol. 11: 1–8.

The results confirm the findings of Hobmaier & Hobmaier that the lungworm of sheep requires an intermediate molluscan host. Two additional molluscs serve as intermediate hosts, the slug *Milax sowerbyi* and the snail *Hyalinia cellaria*. The free-living larvae resist desiccation up to 1 week. The common black slug *Arion ater* does not transmit this lungworm because the larvae are unable to reach the infective stage. No preference is shown for any particular one of the hosts. Molluscs are more abundant in the lowlands, and were not found on the mountain summits.

Friend, G. R. (1941). 'The life-history and ecology of the salmon gill-maggot *Salmincola salmonea* (L.) (Copepod Crustacean).' Trans. Roy. Soc. Edinb. 60: 503–41.

As fry, parr and smolt, salmon are never parasitized by gill-maggots, nor are they in the first sea phase. However, on return to spawn in the river they become infected by the free-swimming larvae and in the second sea phase carry gill-maggots which continue to thrive and grow but not to reproduce. These once spawned fish are thus not infective in the sea but become so when they return to spawn a second time.

Rothschild, M. & Sproston, N. G. (1941). 'The metacercaria of *Cercaria doricha* Roths. 1934, or a closely related species.' Parasitology, 33: 359–62.

Active metacercaria, probably of *C. doricha*, were obtained from *Gadus luscus* (pout). This discovery narrows down the search for the final host to a comparatively few predator fish.

Turk, F. A. (1942). 'Phoretic mites on *Bombus jonellus* Kirby (Hym.).' Ent. Mon. Mag. 78: 51.

Nymphs of *Gamasus nidicolens* and *G. bombianus* found on bumble bees in Cornwall.

Imms, A. D. (1942). 'On *Braula coeca* Nitsch and its affinities.' Parasitology, 34: 88–100.

Material in all stages is obtainable during the months July to November after which only adults occur. The larva is an inquiline which mines for itself a burrow on the underside of the capping of the honey cells of the hive bee. The structure of larva and pupa is described. The larva is structurally similar to that of the Chamaemyiidae, indicating close relationship though the imagines have undergone very divergent evolution.

Kassanis, B. (1942). 'Transmission of potato virus Y by *Aphis rhamni* (Boyer).' Ann. Appl. Biol. 29: 95.

A. rhamni is as efficient a vector of potato virus Y as *Myzus persicae* and it reacts to a preliminary starving period in the same way.

Baker, F. (1942). 'Microbial synthesis and autolysis in the digestive tract of Herbivora.' Nature, Lond. 149: 582–3.

In the rumen of ruminants and caecum of non-ruminant Herbivora are many species of bacteria which play an important part in breaking down starch, pectins and cellulose. These bacteria are themselves broken down and eventually utilized by the host. A variety of agents are responsible, including Protozoa. In the adult rabbit, however, Protozoa may be altogether absent, and in such cases autolysis is important in eliminating the starch-containing microflora—which are rarely to be found in the faeces.

4. FOOD AND FOOD HABITS

Portal, M. (1942). 'A foe to young trees.' Country Life, 26 June, 91: 1235.

General article, apparently including a few original notes, on tree-damage done by the American grey squirrel (*Sciurus carolinensis*) in this country. Excellent photographs of damaged and undamaged pine shoots and fir-cones.

Taylor, E. L. (1941). 'Pseudo-rumination in the rabbit.' Proc. Zool. Soc. Lond. A, 110: 159–63.

A very sharp change-over was noted between the production of wet and dry faeces. The former are swallowed at once and remain in the cardiac portion of the stomach for a considerable time. The probable advantage of the process is the manufacture and digestion of bacterial protein.

Baggaley, W. (1942). 'The larder of a pair of red-backed shrikes.' Brit. Birds, 35: 170–3.

Three pairs of birds used 22 thorn bushes all through the season. Prey found were nine young whitethroats, one young hedge sparrow, over 100 moths and bees and several dor-beetles, cockchafers and grasshoppers.

Collinge, W. E. (1941). 'The food of the blackbird (*Turdus merula* L.) in successive years.' Ibis, 5: 610–13.

Percentage figures are given (actual numbers not stated) for the composition of food of the blackbird in 1933, 1934, 1938 and 1939, and these are contrasted with previous work done in 1924–7. A fall from 25·5 % to about 15 % is recorded in cultivated fruits taken and a rise in insects from 22 to 30 %. It is suggested that a diminution in the numbers of blackbirds is responsible.

Smith, S. (1942). 'Field observations on the breeding biology of the yellow wagtail.' Brit. Birds, 35: 186–9.

A short account, mentioning that food brought for the young was mostly small Diptera, including craneflies, black and green Aphids and small beetles.

Thomas, J. F. (1942). 'Report on the redshank inquiry 1939–40 organised by the British Trust for Ornithology.' Brit. Birds, 36: 5–14, 22–34.

Evidence that up to 1866 the redshank bred almost exclusively on the east side of England, in the north of Scotland and in various parts of Ireland. By now there are only four or five counties in which it does not breed. Notes on winter distribution, breeding habitats, breeding biology and food. Analysis of a number of pellets from Carmarthenshire collected in May and June showed that Amphipod and Isopod Crustacea formed most of the food. Insects, especially beetles, and Gastropod molluscs were also fairly commonly found. In the winter Decapod Crustacea formed the bulk of the pellets and molluscs were more numerous than in spring, but insects were rare.

Myers, C. (1942). 'Trout and microscopic food: a study of trout growth in Wyresdale Lake.' Salm. Trout Mag. Lond. No. 104: 28–31.

Up to 1933 this lake was annually stocked with 2- and 3-year-old fish from hatcheries. The average weight of fish caught was 8 oz. Since 1933 it has been stocked only with fry and the average weight of fish caught has risen to over 12 oz. This change is ascribed to a change in feeding habits. Hatchery-fed fish are used to food particles of a considerable size and when introduced into the lake ignore the abundant supplies of planktonic animals and try to feed on *Asellus, Planorbis* and Chironomid larvae, which are not very plentiful. Fry learn to eat plankton and the habit is continued throughout life.

Goodliffe, F. D. (1942). 'Studies on insects bred from barley, wheat, maize and oats.' Bull. Ent. Res. 32: 309–25.

Miscellaneous notes concerning the occurrence, food habits and parasites.

Niblett, M. (1942). 'Notes on some gall-causing Cecidomyidae: II.' Entomologist, 75: 14–16.

Records of gall midges attacking Salicaceae.

Niblett, M. (1942). 'Notes on some gall-causing Cecidomyidae: III.' Entomologist, 75: 42–5.

Records of galls on *Stachys silvatica, Rosa* spp., *Polygonum amphibium, Veronica chamaedrys, Galium* spp., *Bryonia dioica, Viola* spp., *Epilobium angustifolium, Trifolium repens, Spiraea ulmaria,* and *Urtica dioica.*

Niblett, M. (1942). 'Notes on some gall-causing Cecidomyidae: IV.' Entomologist, 75: 109–12.

Galls on *Spirea ulmaria, Fraxinus excelsior, Urtica dioica, Linaria vulgaris, Helianthemum chamaecistus, Silaus flavescens, Daucus carota, Lotus corniculatus, Tragopogon pratense, Senecio* spp., *Scrophularia nodosa, Solanum dulcamara, Clematis vitalba,* other Umbelliferae, *Achillea millefolium, Erigeron acre,* etc.

Singh, B. N. (1942). 'Selection of bacterial food by soil flagellates and amoebae.' Ann. Appl. Biol. 29: 18–22.

The food preferences of two soil amoebae and a soil flagellate, *Cercomonas crassicauda,* were compared as regards forty-eight strains of bacteria, which include a miscellaneous group mostly from soil, a group of *Rhizobium* strains and a group of plant pathogens. The amoebae were able to eat about half the strains belonging to the miscellaneous group of mostly soil bacteria, most of the plant pathogens, but not the strains of *Rhizobium*. The *Cercomonas* however could eat all the strains of plant pathogens.

5. POPULATION STUDIES

Venables, L. S. V. & Leslie, P. H. (1942). 'The rat and mouse populations of corn ricks.' J. Anim. Ecol. 11: 44–68.

Records were obtained of the numbers of rats (*Rattus norvegicus*) and house-mice (*Mus musculus*) at threshing time in 518 ricks in 266 rick groups in Oxfordshire and Berkshire in the seasons of 1939–40 and 1940–1. Numbers of rats rose to a peak in April. During the winter the percentage of adult female rats pregnant in the ricks was 28 as compared with only 3 in females from other environments. The mouse census was less accurate than that for the rats, but sufficient to show that in ricks mice are as serious a problem as rats. Predators were found in ricks containing high rodent populations. The results support the view that the corn rick is a major habitat of rats, both for numbers and amount of breeding, and stress the importance of early threshing and killing all rats found.

Chitty, D. (1942). 'A relative census method for brown rats (*Rattus norvegicus*).' Nature, Lond. 150: 59–60.

Surplus baiting with wheat was used to measure the food consumption of brown rat populations in the field, in connexion with quantitative testing of field control methods for rats. It may be applicable to other species of small mammals. It forms a useful census method if the total food intake of the species is also known, and if it can also be shown that the bait forms the sole food during the period of measurement. Brown rat populations are particularly difficult to measure in the field by any other method.

Elton, C. (1942). 'Voles, mice and lemmings.' 496 pp., 1 plate and 22 text-figures. Oxford.

A general survey of rodent fluctuations, especially 'mouse plagues', in different parts of the world. Includes, from earlier records, a fairly complete description of vole plagues on the Scottish Border in 1875–6 and 1891–2 (ch. 7); and an account of field and laboratory work on mouse and vole populations organized from Oxford between the years 1925–39 (chs. 8 and 9).

Ranson, R. M. (1941). 'Pre-natal and infant mortality in a laboratory population of voles (*Microtus agrestis*).' Proc. Zool. Soc. Lond. A, 111: 45–57.

A method is described for counting embryos in live pregnant voles from the tenth to the seventeenth days of pregnancy. Allowing for errors in the method the approximate mortality from the tenth day to birth is 21%, and from birth to weaning 14%. These rates are unevenly distributed over the population considered.

Warwick, T. (1941). 'A contribution to the ecology of the musk-rat (*Ondatra zibethica*) in the British Isles.' Proc. Zool. Soc. Lond. A, 110: 165–201.

A complete account of the campaign from 1933 to 1935 to exterminate the musk-rat in Britain, with figures on distribution, habitats, catches, weights, growth, embryo rate, sex ratio, foods, etc. Little difference was noted between its habits in this country and in its natural home.

Colquhoun, M. K. (1942). 'The habitat distribution of the grey squirrel (*Sciurus carolinensis*) in Savernake Forest.' J. Anim. Ecol. 11: 127–30.

Sample counts of numbers seen per hour walking at a constant speed are considered reliable for comparing densities in any given season. In mixed forest with oak dominant a preference was shown for beech; in pure beech there may be competition between squirrels and jackdaws (*Corvus monedula*).

Matthews, L. Harrison (1941). 'Reproduction in the Scottish wild cat, *Felis silvestris grampia* Miller.' Proc. Zool. Soc. Lond. B, 111: 59–77.

An account based on 32 specimens. Sexual maturity is reached in 10 (male) and 12 (female) months and the male is then continuously fecund. The female has two litters a year and rarely a third in the winter.

Alexander, W. B. (1942). 'The index of heron population, 1941.' Brit. Birds, 35: 210–13.

Population still shows an overall decrease (*c*. 5%), though there are slight increases in some areas (e.g. Cheshire and S. Lancs.).

Lack, D. & Light, W. (1941). 'Notes on the spring territory of the blackbird.' Brit. Birds, 35: 47–53.

Study of a small number of birds (38) showed that territories were about 2 acres in extent and that territorial disputes were usually settled by threat display involving the colour of the inside of the mouth.

Colquhoun, M. K. (1942). 'Notes on the social behaviour of blue tits.' Brit. Birds, 35: 234–40.

A study of winter flocks with coloured rings, showing that these consist only in part of wandering birds, the rest being residents that are paired already. Dominance relationships are discussed.

Course, H. A. (1941). 'Some census work on the corn bunting.' Brit. Birds, 35: 154–5.

On 6 square miles of chalk country on the border of Hertfordshire and Cambridgeshire (mostly arable) 72 singing males were counted, distributed with a bias in favour of the more flat portions.

Glegg, W. E. (1942). 'A comparative consideration of the status of the hoopoe (*Upupa epops epops* Linnaeus) in Great Britain and Ireland over a period of a hundred years (1839 to 1938) with a review of breeding records.' Ibis, 6: 390–434.

A diffuse analysis of occurrences showing that these birds have decreased during the period concerned and that the proportion spring/autumn records is greater in the south than in the north of Britain.

Hutton, J. A. (1942). 'Recovery of the Wye: forty years of endeavour and its results.' Salm. Trout Mag. Lond. No. 104: 49–58.

Up to 1902 the salmon fishery of the Wye was ruthlessly exploited for commercial purposes and the stock declined continuously. Then netting was stopped in fresh water and severely restricted in tidal waters, with the result that the average annual catch is now double that at the beginning of the century and the rod catch, for which statistics are incomplete, has probably increased tenfold. This has been achieved without recourse to artificial stocking.

Harle, T. G. A. & Brooks, R. (1942). 'Practical mechanics of trout-scale reading: a new apparatus for easy measurement.' Salm. Trout Mag. Lond. No. 104: 59–63.

A description, with figures, of a new apparatus designed to enable the measurement of the annual growth rings of fish scales to be made in any units at sight.

Myers, C. (1942). 'Elver catching in Lancashire: how the second year's experiment panned out.' Salm. Trout Mag. Lond. No. 104: 46–8.

A description of the apparatus used to trap elvers in the Wyre and Lune, an experiment designed to restrict the eel population in the interests of salmon and sea-trout fisheries.

Bullough, W. S. (1941). 'The effects of the reduction of light in spring on the breeding season of the minnow (*Phoxinus laevis* Linn.).' Proc. Zool. Soc. Lond. A, 110: 149–57.

Reduction of light in spring retarded, but did not inhibit, sexual development.

Barnes, H. F. (1942). 'Studies of fluctuations in insect populations. IX. The carrot-fly (*Psila rosae*) in 1936–41.' J. Anim. Ecol. 11: 69–81.

Yearly abundance was assessed satisfactorily by recording the number of larvae and puparia collected per hour. Emergence, in the collected material at the outdoor insectory at Harpenden, showed a very abrupt peak about 14 May. Average parasitism, except in 1940, was low. Control by treating the bases of carrot clamps with formalin solution is recommended. It is suggested that material from all carrot growing areas be reared at a central station, which would then warn each area by telegram when the fly start emerging. The same could be done for other insect pests the control of which depends on an exact knowledge of dates.

Colquhoun, M. K. (1942). 'A natural population of *Coccinella septempunctata* in Norfolk.' Entomologist, 75: 40–1.

Relative density was estimated by counting all beetles seen during a time period of 15 min. while moving slowly through the herbage. Absolute density, determined by metre quadrat, gave 10–11,000 ladybirds per acre in a lupin and *Atriplex* field where the greatest concentration was noted, and 8000 beetles per acre in a conifer plantation.

Oldham, C. (1942). 'Auto-fecundation and duration of life in *Limax cinereo-niger*.' Proc. Malacol. Soc. Lond. 25: 9–10.

Slugs bred from eggs had a maximum life span of 5 years 270 days. Three isolated slugs all laid fertile eggs.

Oldham, C. (1942). 'Notes on *Geomalacus maculatus*.' Proc. Malacol. Soc. Lond. 25: 10–11.

Two slugs, collected when young, died aged 6 years 117 days and 6 years 137 days, the length of life before collection being estimated. Four slugs hatched from eggs have lived nearly 4 years and are still alive.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Salisbury, E. J. (1942). 'The weed problem.' Nature, Lond. 149: 594–7.

Certain weeds take up rare elements from the soil in much larger amounts than crop plants do and may contain sufficient to prove toxic to livestock. Because of its high molybdenum content white clover is a weed in the 'teart' pastures of Somerset, Gloucester and Warwick. Weeds may be alternative host plants for insect pests, e.g. the turnip flea beetle is harboured by charlock. The abundance of different weeds has varied with the places of origin of the crop seeds they are mixed with, e.g. *Anagallis coerulea* and *Adonis autumnalis*, now rare, came from southern Europe. Many weeds seeds are spread by man's actions, on boots, clothes (e.g. trouser turn-ups), wheels, motor tyres. The wayside pineapple weed (*Matricaria suaveolens*) from Oregon was probably spread very quickly in this country by man or his vehicles. Some seeds survive to be carried in manure.

Anon. (1942). 'Re-appearance of coypus in Hampshire.' The Field, 13 June, 179: 636.

Escapes from fur farms had established in the Blackwater River several years ago. Further damage reported this year, by burrows in grass fields near the stream. Two females trapped, one containing seven young.

Cowin, W. S., Megaw, B. R. S. & Megaw, E. M. (1941). 'Successful breeding of the fulmar petrel in the Isle of Man.' Northw. Nat. 16: 322–4.

Three young reared from five eggs laid on the ledges at Kione ny Ghoggan. First egg seen 22 June 1941.

Southern, H. N. (1941). 'The spring migration of the red-backed shrike over Europe.' Brit. Birds, 35: 114–19.

This shrike comes into Europe from the south-east corner and the isolines showing the rate of spread reflect this origin, and show that progress is made faster along the coast lines than across country. No correlation between the isolines and the isotherms is evident.

Anon. (1942). 'Influx of rare winter birds into Britain.' Nature, Lond. 149: 378.

Summarizes several references to uncommon birds visiting this country as a result of the severe winter 1940–1.

Williams, C. B., Cockbill, G. F., Gibbs, M. E. & Downes, J. A. (1942). 'Studies in the migration of Lepidoptera.' Trans. R. Ent. Soc. Lond. 92: 101–283.

Gives account of progress since the publication of Williams's *Migration of Butterflies* in 1930, an estimate of the abundance each year for over 100 years for about 40 British immigrants, an analysis of nearly 400 records from lightships off the east and south-east coasts of Britain, records of an almost continuous daily watch for nearly 2 years on the movements of butterflies in Florida, the migrations of the milkweed butterfly with full list of British and European appearances, summaries on the migration of several other butterflies from America, Europe, Africa and Australia, experiments in marking butterflies, discussion of orientation in relation to migration, evidence for the occurrence of return flights, correlation between occurrence in unusual numbers of the painted lady butterfly in both Europe and North America, correlation between records of 35 British immigrant species, a method of recording density of flight, and an exhaustive bibliography.

Danreuther, T. (1942). 'Migration records, 1941.' Entomologist, 75: 55–63.

Includes annual totals 1933–41 and totals of representative species recorded in 1941 from eleven stations.

Shepherd, J. (1942). '*Papilio machaon* in Kent.' Entomologist, 75: 46.

A fertile female swallow-tail butterfly captured in a garden at Herne Bay on 26 July 1941; another recorded at Eastry on 25 June. Twelve larvae on carrots found at Ash in August 1940 produced adults in 1941. These were liberated and may have been source of the Eastry specimen. 'Four years ago' one was seen flying in Blean Woods near Herne Bay.

Gordon, S. (1942). 'Wild life in the Western Highlands.' Nature, Lond. 150: 12–13.

Casual notes on effects of the War on wild life, e.g. increase of foxes as result of less game-preservation, and consequent killing of lambs. Believes that bumble bees ('the common bumble bee'...) fly across from mainland to Skye, and from Skye to Lewis.

Baker, F. T., Ketteringham, I. E., Bray, S. P. V. & White, J. H. (1942). 'Observations on the biology of the carrot fly (*Psila rosae* Fab.): assembling and oviposition.' Ann. Appl. Biol. 29: 115–25.

Newly emerged flies remain assembled in large number for about 3 weeks in the hedges surrounding the previous year's crop. Dispersal for oviposition is general and influenced by the wind. The greatest concentration of eggs is close to the hedges.

7. REPORTS OF ORGANIZATIONS

British Trust for Ornithology (1942). Eighth Report for the year 1941. 16 pp.

Reports on progress are given for field inquiries. The organization of the wood pigeon investigation is explained and an appeal made for help. A collection of aerial photographs of coastal and island sea bird colonies taken by Coastal Command of the R.A.F. has been started. This has already yielded information about the species breeding on Rockall, fulmars on the Flannans and gannets on the Scar Rocks.

Clifton College Scientific Society [1942]. The annual report 1941. 23 pp.

Notes on resident and migratory birds, Lepidoptera and plants of the Bude district, Cornwall.

Hutton, J. A. (1942). 'Wye Salmon, 1941: report of the Wye Board of Conservators.' Salm. Trout Mag. Lond. No. 105: 153–67.

Owing to the war no scales for the determination of the age composition of the Wye salmon stock in 1941 were collected, but very careful statistics of the weight of fish caught enables a good estimate to be made. In spite of less intensive fishing, the total catch of 3428 fish weighing 56,111½ lb. was greater than the previous year. Both grilse (fish which have spent only 1 year in the sea) and large spring fish (which have spent 3 years in the sea) were more numerous than the average for the last 30 years.

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